

COMMONWEALTH BUREAU OF HELMINTHOLOGY,

THE WHITE HOUSE,

103, ST. PETER'S STREET,

ST. ALBANS, HERTS.

JOURNAL
OF
HELMINTHOLOGY

(Founded by R. T. LEIPER)

Vol. XXXIII, 1959

Edited by

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and
Tropical Medicine
Keppel Street
London
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A Revision of the Nematode Genus *Setaria* Viborg, 1795, its Host-parasite Relationship, Speciation and Evolution

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INTRODUCTION AND REVIEW OF LITERATURE

Several species of *Setaria* are of veterinary importance, and their records date back to pre-Linnaean days. There is an extensive list of probable synonyms but few of them can be verified with much certainty. Stiles (1907) in a brief review of the genus *Filaria* s.l. recognised several subgenera such as *Hamularia* Treutler, 1793, *Loa* Stiles, 1905, and *Filaria* Mueller, 1787. The equine worm he placed as *Filaria (Hamularia) equina*. He quotes Linstow and Braun as authorities for accepting *Hamularia lymphatica* as identical with *Filaria equina*, and accepts their synonymy. Railliet and Henry (1911a), however, did not agree that *Gordius equinus* Abildgaard, 1789 and *Hamularia lymphatica* Treutler, 1793 were the same. They expressed the opinion that the genus *Setaria* Viborg, 1795 should be used for the equine abdominal cavity worm, although Viborg erroneously associated in the group the body cavity parasites of Apes and Falcons. Therefore *S. equina* should be the type and they made the following combinations :

S. equina (Abildg., 1789), *S. labiato-papillosa* (Alless., 1838), *S. digitata* (Linst., 1906), *S. bidentata* (Molin, 1858), *S. scalprum* (Linst., 1908), *S. cornuta* (Linst., 1899), *S. bicoronata* (Linst., 1900), *S. caelum* (Linst., 1904), *S. transversata* (Linst., 1907), *S. effilata* (Linst., 1897), and *S. (?) spelaea* (Leidy, 1875).

Since then the genus *Setaria* has remained essentially as defined by Railliet and Henry, although later authors have added a number of species.

Boulenger (1921) redescribed two species and added two new species. He redescribed *S. labiato-papillosa* from domestic cattle and the Bush-buck in East Africa, and from the Stag, *Cervus hippelaphus* in Mauritius. In a collection of material from domestic cattle in Burma, he redescribed the female of *S. digitata* and found among those worms a single female specimen with bifurcated lateral lips for which he proposed the name *S. marshalli* after the collector. The fourth species he dealt with is the large species from the Sable Antelope *Hippotragus niger* from Northern Rhodesia which he named *S. hornbyi* after the collector. He stated that Mr. Hornby had seen similar parasites in the Eland, Water-buck and Reed-buck. From the present studies it seems that his *S. labiato-papillosa* is a composite of three species. It is fortunate that his much-reproduced drawings belonged to *S. labiato-papillosa* from cattle. His Bush-buck

parasite is probably *S. africana* n. sp. but the specimens from the Stag are very unlikely to be *S. labiato-papillosa*. His *S. digitata* is a good redescription, while his *S. marshalli* is an abnormal specimen of the same species. His *S. hornbyi* is a good species which unfortunately has not been correctly determined in subsequent literature more than once or twice. From Mr. Hornby's ambiguous statement of "similar parasites", it will be correct to infer them to be *Setaria* s.l., but certainly not *Setaria hornbyi*.

Vevers (1923) records, from animals dying at the London Zoo, *S. hornbyi* from *Hippotragus equinus*, a new species *S. javensis* from *Tragulus stanleyanus*, and a related genus *Papillosetaria*. *S. javensis* was described on female specimens only. It is a very slender, primitive looking worm.

Ortlepp (1924) worked on a collection of helminths from Dutch Guiana. He records *S. labiato-papillosa* from cattle, and a new species, *S. nudicauda* from "some species of deer". His material of the new species consists of a single female specimen of which "the peri-buccal cuticular ring is unfortunately incomplete, its ventral and lateral parts being absent . . . the tail which is smooth . . . terminates in an obtuse tip." The type specimen shows an incomplete peribuccal ring, and the tail, not only smooth, but minus *cauda*. As the specimen has an incomplete head as well as an incomplete tail, the species is unrecognisable. We propose that the species be a *nomen dubium*, and it should not be available for taxonomic purposes.

Thwaite (1927) in a paper entitled "The Genus *Setaria*" redescribed *S. equina*, *S. labiato-papillosa*, *S. hornbyi*; reproduced earlier descriptions and drawings of *S. digitata*, *S. marshalli*, *S. congolensis*, *S. bernardi*, *S. javensis*, *S. nudicauda*, *S. bicornata*, *S. caelum*, *S. cornuta*, *S. scalprum*, *S. transversata*, *S. bidentata*, *Filaria effilata*, *F. spelaea*; and described five new species, (1) *S. pouloni* from Kongoni (*Bubalis lelwel jacksoni*) and Topi (*Damaliscus tiang*), from Uganda, (2) *S. southwelli* from *Cephalophus* sp. from Sierra Leone, West Africa, (3) *S. boulengeri* from *Cervicapra fulvorufula* from Transvaal, South Africa, (4) *S. pillersi* from *Cobus vardoni*, N. Rhodesia, and (5) *S. yorkei* from Impala (*Aepyceros melampus*) and Bush-buck (*Tragelaphus scriptus*) N. Rhodesia. This work was the first compilation of the genus since Railliet and Henry (1911a). His work served the purpose of many workers for a number of years, and still does today. He made some contribution to the genus, and at the same time added some confusion. He redescribed *S. hornbyi* to show

the wide variation in the species, but unfortunately he was not dealing with *S. hornbyi* alone but with several different species.

Raevskaya (1928) published a paper on *Setaria* and its pathogenic importance. This paper appeared early in the year, while that of Thwaite's appeared late in the previous year; the systematic ground covered was much the same in both papers. Raevskaya described two new species in the Soviet Union, *S. tundra* Isachikov and Raevskaya, 1928 in *Rangifer tarandus* in Arkhangelsk, and *S. altaica* Raevskaya, 1928 in *Cervus canadensis asiaticus* in Altai-Shebalino; he redescribed *S. equina* and *S. labiato-papillosa* and reproduced drawings and descriptions of all the species known at that time. In an addendum, he reproduced a summary of Thwaite's five new species. His drawings are the best yet produced on the genus.

In the same year Sandground (1928) published a new species *S. loveridgei* in *Procavia brucei prittwitzi* in Tanganyika Territory. This was the first record of a *Setaria* in hyracoids. In his description he overlooked the long spicule. Baylis (1932a) described a new species, *S. hyracis* in a Tree-Hyrax, *Dendrohyrax* sp. from the Belgian Congo, the second species in hyracoids. He remarked that according to the published description of *S. loveridgei* it is different, especially when the spicules are compared. Sandground (1933a) in a later communication, studied further collections from the hyrax and placed *S. hyracis* as a synonym of his species and rectified his earlier mistake on the long spicule. This synonymy is supported by the present studies.

Maplestone (1931) described a new species, *S. cervi* from the Hog Deer, *Cervus axis* from animals dying at the Calcutta Zoo. Baylis (1936) showed this name to be preoccupied by *S. cervi* (Rudolphi, 1819) which he considered as conspecific. The present investigation shows that *S. cervi* Maplestone (1931) is a synonym of *S. altaica* Raevskaya, (1928).

Purvis (1931) in a short communication concluded that *S. labiato-papillosa* and *S. digitata* were synonyms. His conclusion was both supported and questioned by later workers.

Mönnig (1933) described a new species, *S. thwaitei* from the Sable Antelope, *Hippotragus niger* (type host), the Roan Antelope, *Hippotragus equinus*, and the Water-buck, *Cobus ellipsiprymnus*. His only reference quoted was Thwaite (1927) and he could not have realised

that *S. thwaitei* was conspecific with *S. hornbyi* as described by Boulenger. The present investigation shows that Mönnig, like all the other authors (with the exception of Vevers, 1923), wrongly identified *S. hornbyi*. Kreis (1938) described a new variety, *S. hornbyi* var. *brevicaudatus* from *Hippotragus* sp. from Angola. The latter worm is undoubtedly conspecific with *S. hornbyi* Boulenger.

Bhalerao (1933) described a new species *S. buxi* from the hill goat at Muktesar, India. He had only one female specimen. His description and drawings are satisfactory, but with such limited material, it is difficult to judge its validity. It is possibly a synonym of *S. digitata*.

Baylis (1936a) described a new species, *S. sandersoni* from the duiker, *Philantomba melanorhea* from the Cameroons. He mentioned that his species might be conspecific with *S. cornuta* von Linstow, 1899 which was poorly described. In the present paper I have shown that his suspicion was correct. I have, however, preferred to use the name *S. caelum* (von Linstow, 1904) as the types are in good condition and easily recognisable. In contrast, the type of *S. cornuta* consists of only a single complete worm in poor condition and from an unnamed antelope.

In the same year Baylis (1936b) discussed the nomenclature and synonymy of *Setaria labiato-papillosa*. He concluded that the name *S. cervi* (Rud., 1819) is the valid name for the cattle worm, and gave an extensive list of synonyms such as *S. digitata*, *S. altaica*, etc., which are clearly not synonymous. Since the appearance of his publication, the name *S. cervi* has been used, incorrectly in my opinion, in place of *S. labiato-papillosa*. *S. digitata* has been considered as a synonym of the latter species by some authors, and as a valid species by other authors. The present work is not in agreement with Baylis. I have shown that *S. labiato-papillosa* and *S. digitata* are distinct and good species, and believe that *Filaria cervi* Rud., 1819 is some other species. As the type material of *S. cervi* Rud., 1819 is no longer available and as there is no recognisable description, I propose that *F. cervi* Rud., 1819 be a *nomen dubium*.

van den Berghe and Vuylsteke (1936) gave a list of *Setaria* spp. from various animals in the Belgian Congo. The determinations were made from current literature and a number of specific determinations are therefore incorrect. They also described an interesting species from *Potamochoerus porcus* in the Belgian Congo which they

named *Setaria rodhaini* after the collector. This was the third species from pigs. The first was *S. congolensis* Railliet and Henry, 1911 from *Potamochoerus porcus*, in the Belgian Congo, and the second was *S. bernardi* Railliet and Henry, 1911 from the domestic pig in Indo-China. After examining the type specimens of *S. congolensis* and *S. rodhaini*, I am convinced that they are conspecific.

Sandground (1933b) believed *S. congolensis* and *S. bernardi* to be conspecific, while Chatterji (1939) believed them to be separate species. An examination of the types has proved beyond doubt that they are very different. Sandosham (1954) in a paper entitled "Seven new worms from miscellaneous hosts" described only four new worms. He redescribed *S. javensis* from the Mouse-Deer, *Tragulus stanleyanus*, in Malaya, and described a new species *S. thomasi* from the wild pig, *Sus scrofa jubatus* from Pahang, Malaya. He gave an incomplete list of species described since Thwaite's (1927) work. As the description of *S. thomasi* is unsatisfactory, it must be left as *incertae sedis* until a better description and drawings become available.

Chen (1937) described a new species *S. leichungwingi* from the domestic buffalo in Canton, China. Chabaud and Rousselot (1956) placed it as a synonym of *S. cervi* (Rud., 1819). I agree that it is a synonym, but of *S. labiato-papillosa*, not "*S. cervi*."

Klenin (1940) described *S. bovis* from cattle, *Bos taurus* in the Soviet Union. The male remains undescribed. I have been unable to consult the original paper but from the description without figures as given by Skrjabin and Shikhobalova (1948) it appears not unlike *S. labiato-papillosa*.

Sarwar (1946) expressed disagreement with Baylis (1936b) on the synonymy of *S. cervi* (=*S. labiato-papillosa*) and *S. digitata*, and gave some evidence to show their validity. My studies have shown that Sarwar is undoubtedly correct in the distinction of the two species; but apart from the disputed character of the female tail end, the differential characters he enumerates were unfortunately too variable and thus unacceptable, and the validity of the two species therefore remained disputed.

Kadenzii (1948) published in Skrjabin and Shikhobalova (*op. cit.*) a new species, *S. kabargi* from *Moschus moschiferus* in the Soviet Union. This species appears to be conspecific with *S. tundra* which is found in deer in the Soviet Union and throughout North America.

Böhm and Supperer (1955) redescribed *S. tundra* and gave a series of figures to show the *S. cervi* and *S. digitata* type of tail and concluded that *S. labiato-papillosa* and *S. digitata* are synonyms of *S. cervi* (Rud., 1819) Baylis, 1936. I cannot agree with their findings. Their *S. tundra* is not *S. tundra*, but *Artionema hartwichi* sp. nov. which is described later in the present paper.

Chabaud and Rousselot (1956) described two new species and gave a brief review of the known species. Their new species, *S. longicauda* was collected from *Adenota kob* from Brazzaville, and *S. dipetalonematooides* from *Guevei coeruleus*, also from Brazzaville. In the present paper it is shown that *S. longicauda* is a synonym of *S. pillersi*, and that *S. dipetalonematooides* is a valid species.

MATERIAL AND METHODS

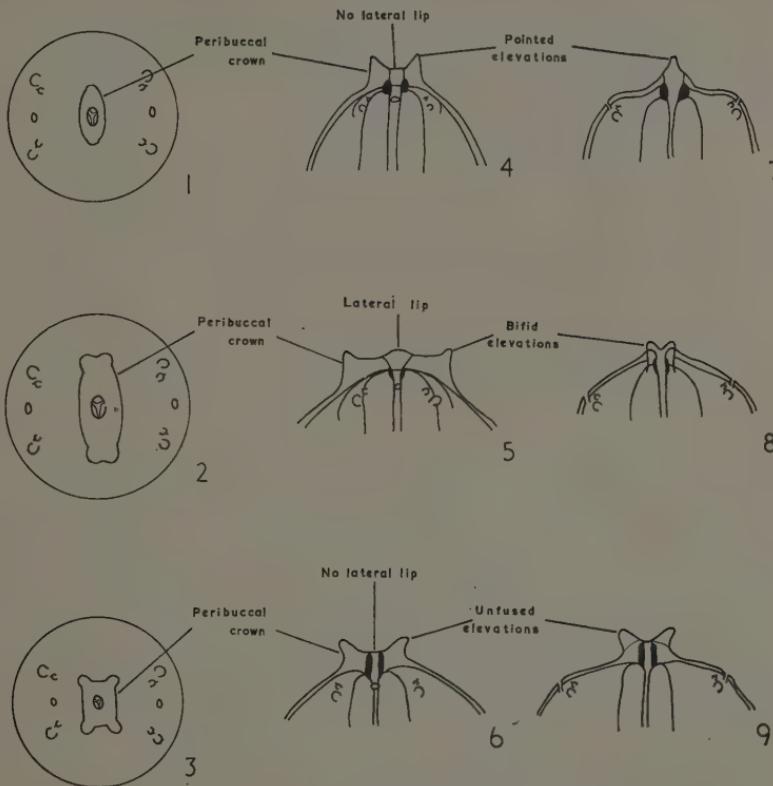
The material available for study is listed under species headings. Every single specimen in the collection was studied, but measurements were taken only for five male and five female specimens taken at random. Where fewer than five specimens of each sex were available, all were measured. Each specimen was studied under different conditions and with different clearing fluids depending on the size and nature of the structures under observation.

KEY TO GENERA OF *SETARIA* S.L.

1. Left spicule stout, head with four prominent spikes, parasites of perissodactyls..... *Setaria* Viborg, 1795
- Left spicule slender, head without spikes..... 2
2. Left spicule long and slender, without long sclerotised membrane, parasites of hyracoids..... *Hyraconema* n.g.
- Left spicule with long sclerotised membrane, parasites of artiodactyls..... *Artionema* n.g.

Hyraconema gen. nov.

Large worms with smooth cuticle. Mouth surrounded by a slightly raised cuticular peribuccal crown upon which are four very small elevations. Head with eight circumoral papillae and two lateral amphids. Cuticularized buccal crown and papillae on a raised



The morphology of the peribuccal crown and its terminology.

Figs. 1-3.—*En face* view of three species of *Actionema*. Figs. 4-6.—Their respective lateral views. Figs. 7-9.—Their respective ventral views.

oval platform whose long axis is laterally situated. Oesophagus is relatively short, and is divided into a thin, short, muscular anterior, and a stout, long, glandular posterior part. *Male*. Ventral surface of male tail with large number of transverse cuticular rugae. Tail with four pairs of precloacal papillae, a single median precloacal papilla, and three pairs of postcloacal papillae. Caudal appendages absent. Spicules very unequal and dissimilar. The short right spicule has a stout proximal and a slender alate distal part. The long left spicule has a pitted shaft and a long sclerotized tubular blade. *Female*. Caudal end coiled into loose spiral with the anal opening on the

convex surface of the curve. Lateral caudal appendages absent. Vulval opening in the oesophageal region with a large muscular ovejector which joins the long uncoiled vagina posteriorly. Vivi-parous.

Adults in peritoneal cavity of hyracoids.

Genotype : *Hyraconema loveridgei* (Sandground, 1928) n. comb.

Syn. *Setaria loveridgei* Sandground, 1928

Setaria hyracis Baylis, 1932

Other species : Unknown

HYRACONEMA LOVERIDGEI (Sandground, 1928) n. comb.

(Figures 10-17)

Syns. and Litt.

Setaria loveridgei Sandground, 1928, pp. 145-7 (In *Procavia brucei prittwitzi*, Tanganyika Territory).

Setaria hyracis Baylis, 1932, pp. 120-3 (In *Dendrohyrax* sp., in Komi, Sankuru, Belgian Congo).

Setaria loveridgei of Sandground, 1933, p. 264 (In *Procavia brucei frommei*).

Setaria loveridgei of Sandground, 1938, pp. 60-1 (In *Procavia brucei frommei*, *P. scheffleri* and *Dendrohyrax* (?) *arboreus* in Kenya, Tanganyika and Belgian Congo).

Material. Type material consisting of two male and two female specimens. (Harvard Museum, U.S.A.).

One female specimen from "Hyrax", Sudan. Coll. Dr. Kirk. (P. L. LeRoux Coll.).

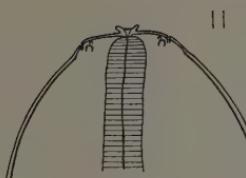
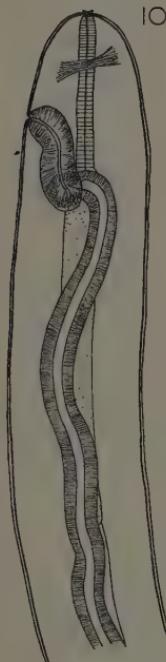
Description. These worms are comparatively slender and very long. The mouth opening is round. It is surrounded by a flat, oblong peribuccal crown slightly upturned at four points to form four small elevations. These elevations therefore look very much alike whether viewed from the ventral, dorsal or lateral aspect. The mouth, peribuccal crown and papillae are all placed on a raised platform, the long axis running laterally.

Female. The female worm is very long, measuring about 300-350 mm. in length and a maximum breadth of 0.6-1.0 mm. The

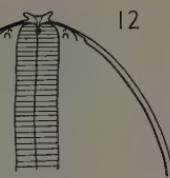
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YEH LIANG-SHENG

11



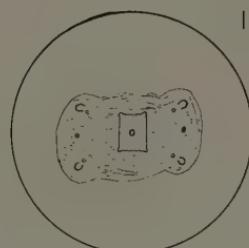
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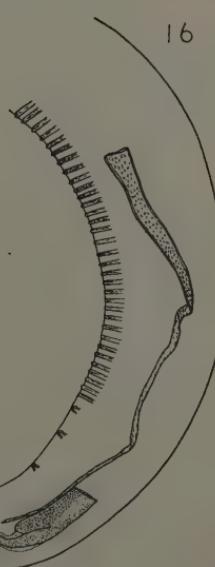
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0.2 mm.

13



17



16



15

0.05 mm.

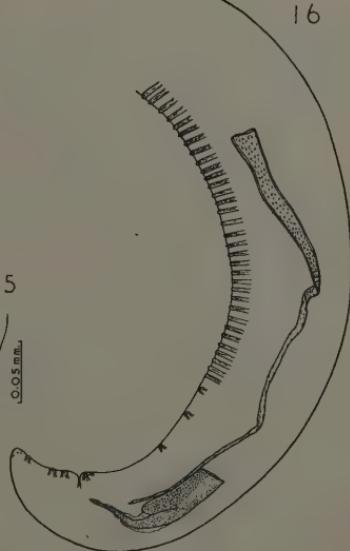
*Hyraconema loveridgei* (Sandground, 1928).

Fig. 10.—Anterior end of female worm. Fig. 11.—Ventral view of head. Fig. 12.—Lateral view of head. Fig. 13.—En face view. Fig. 14.—Female tail. Fig. 15.—Terminal part of female tail. Fig. 16.—Lateral view of male tail. Fig. 17.—Ventral view of male tail. (All drawings from type specimens).

oesophagus is very short, with a total length of only 1.7–2.0 mm., its anterior part measuring 0.4 mm. in length, and the posterior 1.3–1.6 mm. The nerve ring is 0.34 mm. from the anterior extremity. The vulval opening is 0.42–0.45 mm. from the mouth. The long vagina runs posteriorly without coiling. The tail is 0.46–0.62 mm. long and ends in a small knob. There are no lateral caudal appendages, but only a large unpaired tail papilla.

Male. The male is a long slender worm, measuring 132–158 mm. in length and 0.37–0.42 mm. in maximum breadth. The oesophagus has a total length of 1.6–1.9 mm., the anterior part measuring 0.42–0.48 mm. long while the posterior part measures 1.18–1.42 mm. The nerve ring is 0.23 mm. from the anterior extremity. The tail is 0.1–0.13 mm. long. There is a single median precloacal papilla, three pairs of postcloacal and four pairs of precloacal. The anterior-most three pairs of precloacal papillae form a group in themselves and are situated far from the fourth pair. The ventral surface of the male tail end has a number of cuticular rugae.

The right spicule is 0.24–0.26 mm. in length. Its proximal part is stout, while the distal part is slender and alate. The left spicule has a total length of 0.67–0.69 mm., the pitted shaft is 0.25 mm. long, and the tubular blade is heavily sclerotized throughout, and has a length of 0.42–0.44 mm.

Hosts : *Dendrohyrax* sp., *Dendrohyrax* (?) *arboreus*, *Procavia brucei prittwitzi*, *P. brucei frommei* and *P. scheffleri*.

Habitat : Peritoneal cavity.

Locality : Belgian Congo, Tanganyika, Kenya and Sudan.

Discussion. In 1928 Sandground described a new worm, *Setaria loveridgei* from a hyrax, *Procavia brucei prittwitzi* in Tanganyika Territory, East Africa. In that paper, he overlooked the long spicule and the general description and drawings were not entirely satisfactory. Baylis (1932) with only Sandground's description to guide him, described a new worm, *S. hyracis*, recovered from a hyrax, *Dendrohyrax* sp. from the Belgian Congo. Baylis says "it is impossible, however, on the basis of Sandground's description, to consider the two forms identical, for several reasons. The size of *S. hyracis* is somewhat smaller. The number and arrangement of the caudal papillae of the male are quite different, and the spicules are much larger than in *S. loveridgei*, where, according to Sandground, they

measure only 110μ and 50μ in length respectively." Later Sandground (1933a) studied further collections of *Setaria* from the hyrax (*Procavia brucei frommei*, *P. scheffleri* and *Dendrohyrax (?) arboreus*) in Kenya, Tanganyika and the Belgian Congo, and rectified a mistake made in his earlier paper (1928) where he only saw the stout short spicule which he mistook for both spicules. He then showed that *Setaria hyracis* Baylis, 1932 should be placed as a synonym of *Setaria loveridgei* Sandground, 1932. Chabaud and Rousset (1956) accepted the synonymy. The writer had access to Sandground's type specimens and a collection from a hyrax in the Sudan, and agrees that *Setaria hyracis* and *Setaria loveridgei* are conspecific.

Setaria Viborg, 1795

Setaria Viborg, 1795. *Samm. Abh. Thierärzte Oekonomon*, 1
nec Oken, 1815. *Lehrb. Naturg.* 3 (1), Register XV. (Gord.)
nec Blyth, 1844. *J. Asiat. Soc. Bengal*, 13, 385 (Aves)
nec Mulsant & Rey, 1863. *Ann. Soc. linn. Lyon*, 10, 1
(Coleoptera); 1863, *Opusc. ent.*, 13, 1.

Large stout worms. Cuticle at tail end of both sexes is invested with bosses, otherwise smooth. Head with a prominent peribuccal crown with dorsal and ventral elevations and lateral lips. Outside the peribuccal crown are four conspicuous submedian spikes. Still further outside are the eight circumoral papillae and two amphids. The oesophagus is divided into two parts, a short muscular anterior and a long glandular posterior part. *Male*. Tail with caudal alae. Ventral surface of male caudal extremity covered with cuticular bosses. Tail with a single median precloacal papilla, four pairs of precloacal papillae, a single median postcloacal papilla, and five pairs of postcloacal papillae. Spicules stout, unequal and dissimilar. Right spicule short with a bifid tip. Left spicule long with a shaft, blade and a short sclerotized enveloping membrane. *Female*. Anal opening on convex surface of curvature. Lateral caudal appendages present. Tail covered with cuticular bosses. Vulval opening in oesophageal region with large muscular ovejector which joins an uncoiled vagina posteriorly. Viviparous, microfilariae sheathed and found in the blood.

Parasites of equine animals.

Genotype : *Setaria equina* (Abildg., 1789) Railliet and Henry, 1911

Other species : Unknown

SETARIA EQUINA (Abildgaard, 1789) Railliet and Henry, 1911
(Figures 18-25)

Important synonyms :

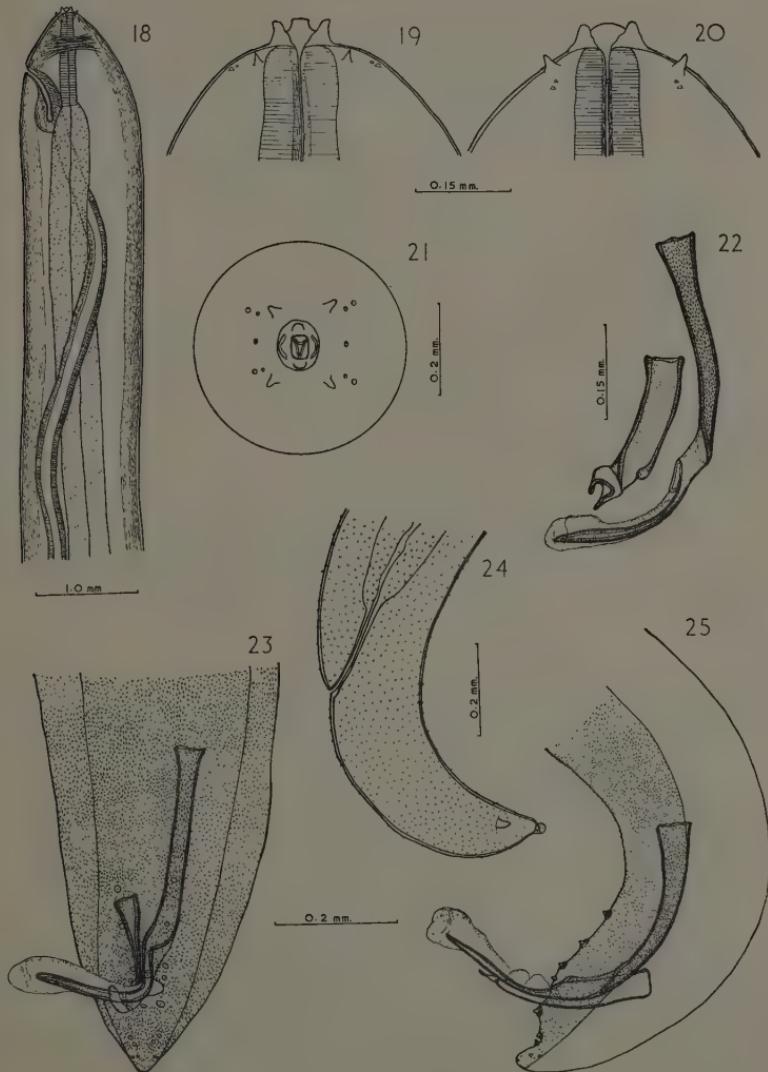
Gordius equinus Abildgaard, 1789; *Filaria equi* Gmelin, 1790;
Filaria papillosa Rudolphi, 1802; *Filaria equina* (Abildg.,
1789) Blanchard, 1849.

Material. 5 females from donkey, N. Rhodesia; 2 females from horse, N. Rhodesia; 1 male from horse, N. Rhodesia. (P.L. LeRoux Coll.). 8 females from horse, Caucasus; 6 females from horse, Egypt; and 7 females from horse, India. (L.S.H.T.M. Coll.). 1 female from mule, Natal (P. L. LeRoux Coll.). 2 females from mule, E. Africa (L.S.H.T.M. Coll.). 1 male and 3 females from zebra, Zululand, 7 females from zebra, Zululand, 5 females and 2 males from zebra, N. Rhodesia, 4 females from zebra, N. Rhodesia (P. L. LeRoux Coll.). 3 females from zebra, Tanganyika (L.S.H.T.M. Coll.).

Introduction. This is the common parasite of equine animals, with practically a cosmopolitan distribution. In spite of being the genotype and of veterinary importance, it has been inadequately described. The material available to the writer is sufficiently good for him to make a reasonable redescription.

Description. These worms are comparatively large, and rather stout for a filarioïd. They taper gradually at both extremities. The mouth opening is square. It is surrounded by a prominent peribuccal crown, slightly dorso-ventrally elongated, and provided with a dorsal and a ventral peribuccal elevation and a pair of lateral lips. The two lateral lips are crescentic in outline, while the dorsal and ventral elevations are truncated. Submedian to these elevations are four prominent spikes which are characteristic. The head is provided with eight circumoral papillæ and two lateral amphids. The union of the oesophagus with the intestine is very obvious in that the diameter of the intestine is much less.

Female. The female is a large worm measuring about 110-130 mm. in length and 1.0-1.2 mm. in breadth. The cuticle of the worm has very fine subcuticular striations, but the surface is smooth. The posterior part of the worm has conspicuous cuticular bosses. The bosses are very dense around the tail region up to about 9-10 mm.



Setaria equina (Abildgaard, 1789).

Fig. 18.—Anterior end of female worm. Fig. 19.—Ventral view of head. Fig. 20—
Lateral view of head. Fig. 21.—En face view. Fig. 22.—Dissected male spicules.
Fig. 23.—Ventral view of male tail. Fig. 24.—Lateral view of female tail. Fig.
25.—Lateral view of male tail.

from the caudal end, and then become more and more sparse and finally disappear when they reach about the posterior third or half of the worm. The oesophagus is 12-13 mm. long, its anterior part measures 0·8-1·0 mm. in length, and the long posterior part is 11-12 mm. long. The nerve ring is 0·25-0·31 mm. and the cervical papillae 0·5-0·6 mm. respectively from the cephalic end. The vulval opening is flush with the body cuticle, 0·48-0·82 mm. from the anterior end. The vagina runs straight back without any coiling for a distance of 10-12 mm. before bifurcation to become the uteri which are packed with sheathed microfilariae.

The posterior extremity of the worm usually has a single coil. The tail region is therefore curved, and measures about 0·34-0·55 mm. in length. The tail ends in a small uneven-surfaced terminal knob. Lateral to this, and 0·06-0·1 mm. from the extremity, there are two lateral appendages.

Male. The male has a length of 51-66 mm. and a breadth of 0·47-0·56 mm. The cuticle is smooth except for the caudal region where the ventral surface is studded with closely packed minute bosses reaching as far up as 1·5 mm. from the caudal end. The small lateral alae run for a number of millimetres before disappearing.

The oesophagus has a length of 6-8 mm., the anterior portion measuring 0·51-0·55 mm. and the posterior portion 5·3-7·3 mm. The nerve ring is 0·19-0·21 mm. and the cervical papillae 0·55 mm. from the cephalic end. The tail is short, being only about 0·11-0·13 mm. long. There are eight pairs of lateral caudal papillae, of which four are precloacal and four postcloacal. There is also a single median precloacal papilla and another single median postcloacal papilla.

The short right spicule measures 0·28-0·29 mm. in length; its distal end terminates in a "claw" through which the longer spicule slides. The left spicule has a length of 0·61-0·64 mm. It has a proximal tubular shaft of 0·31-0·35 mm., then a sharp twist, then a narrower distal blade, 0·26-0·28 mm. long. The blade is completely covered by a sclerotized membrane much larger in diameter and with fine transverse markings. This membrane protrudes for about 30 microns beyond the distal length of the spicule proper. In this species the spicules are often found slightly protruded in the specimens.

Hosts : Donkey, horse, mule and zebra. Also reported from cattle and man, but this needs confirmation.

Habitat : Peritoneal cavity. Also recorded from thoracic cavity, lungs, pleural sac, liver, testicles, stomach, intestine and eyes.

Locality : Practically cosmopolitan.

Discussion. Although *Setaria equina* is a common parasite of equine animals and widely distributed, it has been poorly described, and certainly incorrectly described in veterinary textbooks. It is one of the easier species to identify owing to the four prominent cephalic submedian spikes, and the cuticular bosses on the caudal region of both sexes.

I have examined several collections of *Setaria s.l.* from the aqueous humour of eyes of equine animals, and in every instance, they were not *Setaria equina*, but *S. digitata*. Schwartz (1927) has reported two cases of *S. equina* in eyes of horses in the United States and one case of *S. digitata* in eyes of a horse in Indo-China.

Artionema gen. nov.

Medium to large worms. External surface of body cuticle smooth except for ventral surface of male tail which has transverse rugae, or rugae and bosses. Cuticular layering gives a pseudo-striation throughout. Mouth opening round or elongated, with small buccal capsule and a conspicuous peribuccal crown. Peribuccal crown may be cylindrical and smooth, or with elevations; lateral cuticularized lips present or absent. Anterior extremity with lateral shoulders on which are situated eight submedian papillae and two lateral amphids. Oesophagus consists of two parts, a short muscular anterior, and a long glandular posterior part. *Male*.—Caudal alae of varying size. Caudal appendages present. Ventral surface of male tail with transverse cuticular rugae, or with bosses in addition to rugae. There is a single median precloacal papilla, and eight to ten pairs of pre- and post-cloacal papillae. Spicules unequal and dissimilar. Right spicule short, stout and curved, usually with distal extremity grooved. Long left spicule with shaft, blade and a long protruding sclerotized membrane. Gubernaculum absent. Telamon present. *Female*.—Caudal end slightly coiled with anal opening on the convex surface of its curvature. Caudal appendages

present. Tail ending with knob or spikes. Vulval opening in oesophageal region, muscular ovejector merges on distal aspect into uncoiled vagina. Viviparous, microfilariae sheathed and found in the blood.

Adults in Artiodactyls.

Genotype : *A. africana* n. sp.

Other species : See list in Contents, pp. 1-2.

Key to the species of **Artionema** gen. nov.

- A. Parasites of Tragulidae..... *A. JAVENSIS*
- Parasites of Suidae B
- Parasites of Cervidae C
- Parasites of Bovidae D

- B. Suidae
 - 1. Head without definite elevations *A. CONGOLENSIS*
 - Head with bifid elevations *A. BERNARDI*

- C. Cervidae
 - 1. Head with four elevations *A. ALTAICA*
 - Head with dorsal and ventral elevations 2
 - 2. Female caudal appendages large, tail with terminal spikes *A. TUNDRA*
 - Female caudal appendages small, tail with terminal knob *A. HARTWICHI* n. sp.

- D. Bovidae
 - Parasites of Antilopinae..... *A. SCALPRUM*
 - Parasites of Cephalophiniae DA
 - Parasites of Hippotraginae DB
 - Parasites of Bovinae DC

- DA. Cephalophiniae
 - 1. Dorsal and ventral elevations bifid..... *A. CAELUM*
 - Dorsal and ventral elevations unbranched..... 2
 - 2. Dorsal and ventral elevations smooth and square..... *A. DIPETALONEMATOIDES*
 - Dorsal and ventral elevations pointed..... *A. SOUTHWELLI*

DB. Hippotraginae

- | | |
|--------------------------------------|----------------------|
| 1. Four elevations | <i>A. HORNBYI</i> |
| — Two elevations | 2 |
| 2. With lateral lips..... | <i>A. POULTONI</i> |
| — Without lateral lips | 3 |
| 3. Elevations bifid..... | <i>A. BICORONATA</i> |
| — Elevations unbranched | 4 |
| 4. Elevations smooth and square..... | <i>A. BOULENGERI</i> |
| — Elevations pointed | <i>A. PILLERSI</i> |

DC. Bovinae

- | | |
|--|-----------------------------|
| 1. Female tail with terminal knob | <i>A. DIGITATA</i> |
| — Female tail with terminal spikes | 2 |
| 2. Mouth opening round..... | <i>A. AFRICANA</i> n. sp. |
| — Mouth opening elongated..... | <i>A. LABIATO-PAPILLOSA</i> |

ARTIONEMA JAVENSIS (Vevers, 1923) n. comb.

(Figures 26-34)

Syns. and Litt.

Setaria javensis Vevers, 1923, pp. 911-2 (in *Tragulus stanleyanus*, Java [London Zoo]).

Setaria javensis of Sandosham, 1954, pp. 217-20 (in *Tragulus javanicus*, Malaya).

Material. Type material consisting of 2 female specimens from *Tragulus stanleyanus*, Java, which died in the London Zoo. (L.S.H.T.M. Coll.).

Two females from *T. stanleyanus*, died in London Zoo, and a large number of incomplete specimens from *T. stanleyanus*, Java, died in London Zoo. (L.S.H.T.M. Coll.). Four females and one male from *T. javanicus*, Malaya, and one female and three males from *T. javanicus*, Malaya (kindly sent by Dr. J. F. B. Edeson, Malaya).

Introduction. Baylis and Daubney (1922) recorded a larval *Setaria* sp. from *Tragulus javanicus*, but gave no description. As *A. javensis* is the only species of *Artionema* known in this host, it is quite likely that they were dealing with this species. The species was

described by Vevers (1923) from the Mouse-Deer, *Tragulus stanleyanus* on female specimens only. Sandosham (1954) redescribed this species and gave a description of the male.

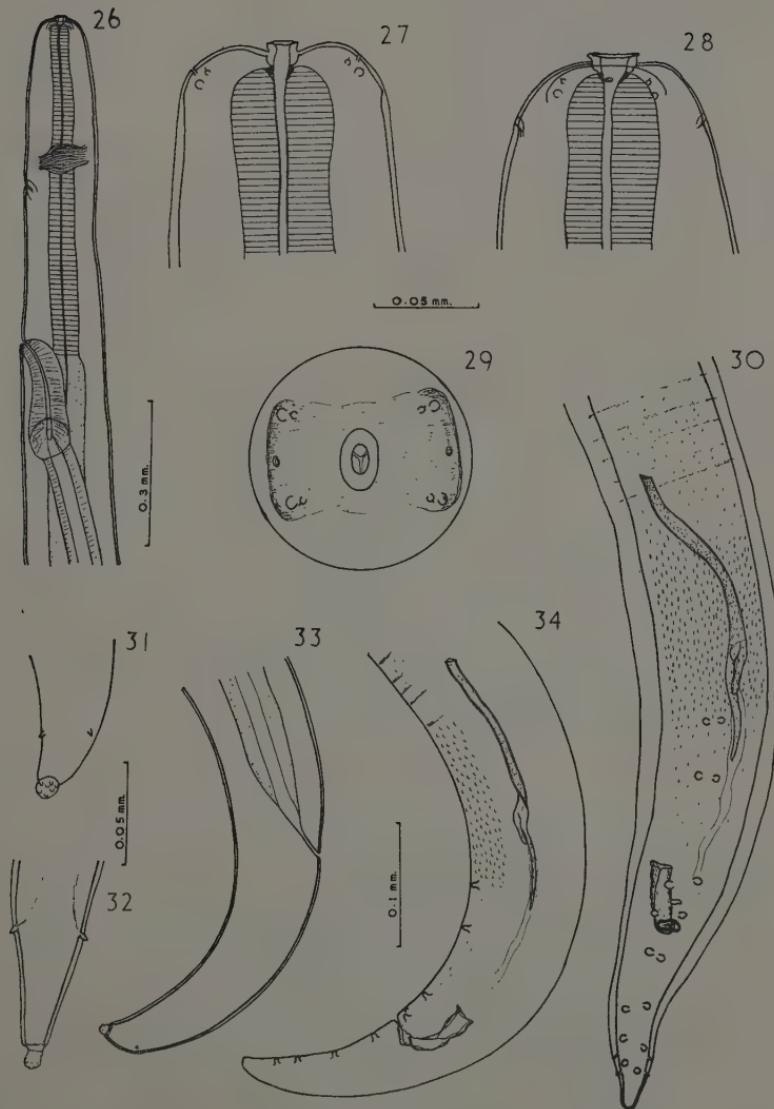
Description. The worm has a smooth cuticle, except for the ventral surface of the male tail end. The mouth has a small buccal capsule, the mouth opening is oval, and the tubular peribuccal crown is formed by the raised body cuticle. The peribuccal crown is a simple oval ring without any ornamentation.

Female. The female has a length of 53–102 mm. and a maximum width of 0·3–0·4 mm. The oesophagus has a total length of 2·1–3·2 mm., the anterior part measuring 0·3–0·6 mm. and the posterior part 1·7–2·6 mm. The nerve ring and cervical papillae are 0·2–0·3 mm. and 0·3–0·6 mm. respectively from the cephalic end. The vulval opening is near the junction of the division of the oesophagus, 0·4–0·65 mm. from the mouth. The tail has a length of 0·24–0·46 mm. and ends in a slightly elongated terminal knob. The distal end of the knob has a number of papilla-like divisions. The diameter of the tail at the anus is 0·06–0·08 mm. The caudal appendages are small, 40–60 microns from the extremity.

Male. The male has a length of 37–41 mm. and a maximum breadth of 0·25 mm. The oesophagus has a total length of 2·2–2·3 mm., the anterior part measuring 0·4–0·5 mm. and the posterior part 1·7–1·8 mm. The nerve ring and cervical papillae are 0·23–0·24 mm. and 0·52 mm. respectively from the cephalic end. The tail is 0·11–0·13 mm. long. On the ventral surface beginning from the anterior-most pair of papillae there are very distinct cuticular bosses. They are very obvious over a distance of about 0·13 mm. and fade away gradually both anteriorly and posteriorly. Immediately anterior to the bosses are very faint transverse cuticular rugae, about twenty in number. There is a single median precloacal papilla, and eight paired papillae of which four are precloacal and four postcloacal. They are not evenly distributed, as there is a very large gap between the second and third pair of precloacals. The curved right spicule is 0·06–0·07 mm. in length. The distal end has a very marked transverse groove. The left spicule has a shaft of 0·14–0·15 mm. and a blade of 0·07 mm. long.

Artionema javensis (Vevers, 1923).

Fig. 26.—Anterior end of female worm. Fig. 27.—Ventral view of head. Fig. 28.—Lateral view of head. Fig. 29.—*En face* view. Fig. 30.—Ventral view of male tail. Figs. 31–2.—Terminal part of female tail. Fig. 33.—Female tail. Fig. 34.—Lateral view of male tail.



- Type host* : *Tragulus stanleyanus*
Other hosts: *T. javanicus*
Habitat: Peritoneal cavity
Type locality: Java
Other localities: Malaya

Discussion. Vevers (1923) described this species from female specimens collected from the Mouse-Deer, *Tragulus stanleyanus* which died in the London Zoo. Recently Sandosham (1954) re-described this species from *T. javanicus* from Malaya. He had one male and three female specimens.

Thwaite (1927) did not examine any specimens of *Artionema javensis*. His criticism (p.457) that Vevers' "figure is not sufficiently clear to enable the exact structure of the mouth parts to be determined in detail" is unjustified. After examining a number of specimens, I consider Vevers' work a reasonably accurate presentation of the worm. Sandosham (1954) with three females and one male specimen did not improve on the description. His description and drawings of the male worm are inaccurate. He says there are no caudal appendages though they are present in the paratype and all our specimens. He also described the male tail cuticle, and noted six pairs of caudal papillae of which four are post-anal. His observations on the cuticle and the number of papillae were far from correct. The male tail cuticle has much interest and is characteristic of the species.

ARTIONEMA CONGOLENSIS (Railliet and Henry, 1911) n. comb.
(Figures 35-44)

Syns. and Litt.

Setaria congolensis Railliet and Henry, 1911, pp. 386-9
(in *Phacochoerus porcus*, Ibenga, French Congo).

Setaria congolensis of Gedoelst, 1916, p. 48 (in *Potamochoerus porcus*, Katanga, Belgian Congo).

Setaria congolensis of Thwaite, 1927, p. 446 (English translation of original description).

Setaria bernardi of Mönnig, 1928, pp. 818-9, 823, 837 (in *Sus scrofa domestica*, Portuguese East Africa).

S. rodhaini van den Berghe and Vuylsteke, 1936, pp. 424-8
(in *Potamochoerus porcus*, Bambili, Belgian Congo).

Setaria congolensis of Baylis, 1939, p. 628 (in *Potamochoerus porcus*, Belgian Congo).

Material. Type material consisting of four excellent permanent mounts with the anterior end of a male, a female, and the lateral view of a male tail and a female tail.

Type material of *Setaria rodhaini* consisting of two males and three females.

One male and one female specimen from the type host, *Potamochoerus porcus*, Belgian Congo (Brit. Mus. Coll., Baylis, 1939). One complete and one incomplete female specimen from the African Bush-Pig, *Potamochoerus koiropotamus*, N. Rhodesia (P. L. LeRoux Coll.).

Introduction. *Setaria congolensis* was described by Railliet and Henry 1911. His material consisted of two males and seven females from the peritoneal cavity of three Red River-Hogs, *Potamochoerus [Phacochoerus] porcus* in the region of Ibenga, French Congo. The description was good, but unaccompanied by drawings. As I had the opportunity of re-examining the type material, I shall give a re-description of the species with drawings. The material from N. Rhodesia constitutes a new host record. The following description is based on three complete worms, one male and two females. (The type material of *Setaria rodhaini* arrived too late to be included).

Description. These are relatively large worms with a thick smooth cuticle. The mouth structures are unique. They consist of a small buccal capsule surrounded by a raised body cuticle forming a cylindrical tube with the free end bending slightly backwards. It therefore consists of two tubes, the cylindrical buccal capsule which seems to be a continuation of the inner lining of the oesophagus and this is surrounded by a second tube formed by the raised body cuticle.

Female. The female worm measures 112-122 mm. in length and 0.6-0.96 mm. in maximum diameter. The oesophagus has a total length of 11-13 mm., the anterior part with a length of 0.9 mm. and the posterior part 10-12 mm. The nerve ring and cervical papillae are 0.19-0.24 mm. and 0.29-0.38 mm. respectively from the cephalic

extremity. The vulval slit is horizontal. It is situated about 0·35–0·38 mm. from the mouth. The vagina proceeds posteriad without coiling. The tail is 0·36–0·56 mm. in length and ends bluntly in an inconspicuous knob and covered by an irregular circle of small spikes around a stouter central spike. Some of these spikes were worn-off in one of the specimens. There is a pair of small papilla-like caudal appendages.

Male. The male has a length of 76 mm. and a maximum diameter of 0·54 mm. The oesophagus has a total length of 12·5 mm., the anterior part measuring 0·8 mm. and the posterior part 11·7 mm. The nerve ring and cervical papillae are 0·26 mm. and 0·45 mm. respectively from the anterior end. The short pointed tail is 0·17 mm. long. There are no definite caudal alae. The ventral surface is covered with a series of cuticular rugae. There is a median pre-cloacal papilla (?paired), and three pairs of precloacal and seven pairs of post-cloacal papillae.

The stout, curved right spicule has a length of 0·14 mm. and has a bent overlapping split distal end. The left spicule has a shaft of 0·21 mm. and a slender pointed blade of 0·13 mm.

Type host : *Potamochoerus porcus*

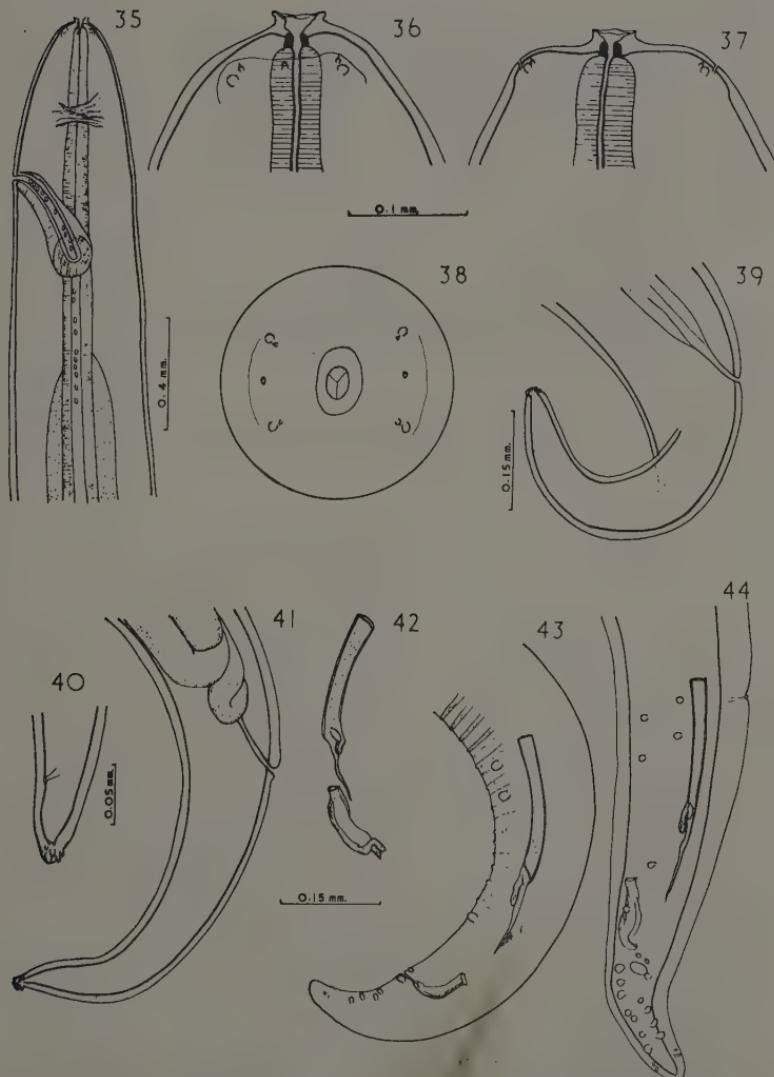
Other hosts: *Potamochoerus koiropotamus* and *Sus scrofa domesticus*

Habitat : Peritoneal cavity

Type locality: Ibenga, French Congo

Other localities : Rhodesia and Mozambique

Discussion. Soon after this species was described by Railliet and Henry (1911a) there appeared in the same year and in the same journal a description of an unnamed *Setaria* sp. from the domestic pig in Indo-China by Bernard and Bauche (1911). Railliet and Henry (1911b) commented on the material and noted its difference from *Setaria congolensis*; they named it after the senior author, *Setaria bernardi*. As there were no drawings, there began a controversy over its validity. Mönnig (1928) had a collection of six females and one male, and identified his material as "(?) *S. bernardi*", and mentioned that they did not agree very well with the original description of *S. bernardi*. He, however, was unaware of the valid



Artionema congolensis (Railliet and Henry, 1911).

Fig. 35.—Anterior end of female worm (Tp). Fig. 36.—Lateral view of head (Tp). Fig. 37.—Ventral view of head. Fig. 38.—En face view. Fig. 39.—Female tail (Tp). Fig. 40.—Terminal part of female tail. Fig. 41.—Female tail. Fig. 42.—Male spicules (Tp). Fig. 43.—Lateral view of male tail. Fig. 44.—Ventral view of male tail. (Tp = type specimen).

species, *Setaria congolensis*. Sandground (1933b) collected three male *Setaria* specimens from *Sus cristatus* in Indo-China and concluded from his study that *Setaria bernardi* Railliet and Henry, 1911b should be placed under synonymy of *Setaria congolensis* Railliet and Henry, 1911. Chatterji (1939) with a collection of *Setaria* from the pig in Burma, disagreed with Sandground on the synonymy; he concluded that the two species *Setaria congolensis* and *Setaria bernardi* were distinct.

Having examined the type material of both species I have no doubt that the two species are quite distinct. The presence or absence of head elevations and the number of tail papillae on the male makes it very easy to differentiate them.

ARTIONEMA BERNARDI (Railliet and Henry, 1911) n. comb.
(Figures 45-49)

Syns. and Litt.

Filaria sp. of Bernard and Bauche, 1911, pp. 482-5 (in domestic pig, slaughter house, Annam).

Setaria bernardi Railliet and Henry, 1911b, pp. 487-8 (redescription and naming of above specimens).

Setaria congolensis of Sandground, 1933, pp. 578-80 (in *Sus cristatus*, Annam).

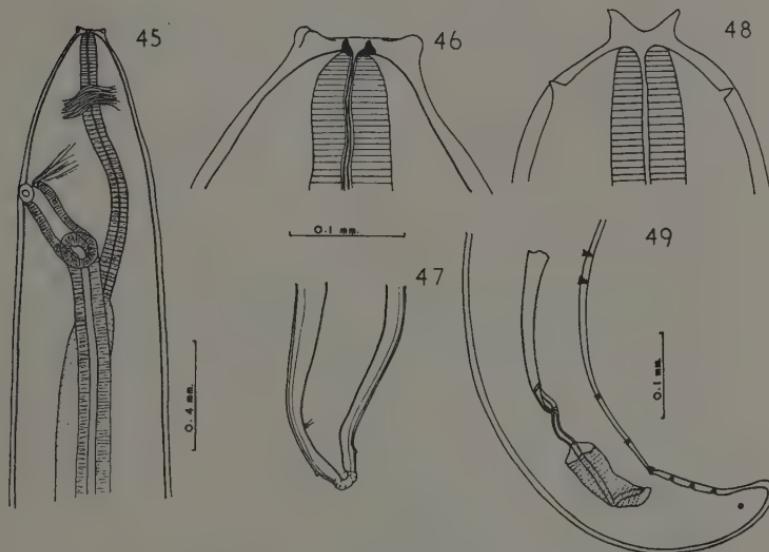
Setaria bernardi of Chatterji, 1939, pp. 327-32 (in domestic pig, slaughter house, Burma).

Material. Type material consisting of two permanent mounts, one with the anterior end and the other the caudal end of a female.

Introduction. As I have not any material other than the type specimens, the following description is essentially that of Chatterji (1939).

Description. (After Chatterji, 1939). Body filiform, cylindrical and attenuated at both extremities, more attenuated posteriorly than anteriorly. Head provided with two lateral and four pairs of submedian papillae. Cuticle with fine transverse striations, inconspicuous at head ends. Mouth enclosed by chitinous peribuccal crown, the dorsal and ventral margins of which are indented whereas the lateral margins are slightly convex, or straight or depressed

antero-posteriorly, the condition varying with the different degree of contraction of the head. Distance between dorsal and ventral projections of peribuccal crown 0·05–0·08 mm. A pair of small lateral papilla-like appendages near tip of tail is present in both sexes.



Artionema bernardi (Railliet and Henry, 1911).

Fig. 45.—Anterior end of female worm. Fig. 46.—Lateral view of head. Fig. 47.—Terminal part of female tail. Fig. 48.—Ventral view of head. Fig. 49.—Lateral view of male tail. (Figs. 45–7.—Drawn from type specimens. Figs. 48–9.—After Chatterji, 1939).

Female. (After Chatterji, 1939). Length 150–180 mm., maximum diameter 0·65–0·75 mm. Muscular oesophagus 0·8–1·0 mm. and glandular oesophagus 9–10 mm. long. Nerve ring at 0·28–0·31 mm. from anterior end. Vulva lying very clearly under a little projection 0·46–0·53 mm. from anterior end and provided with strong sphincter muscles. Vagina approximately 0·3 mm. long, running obliquely posterior and near union of muscular and glandular portions of oesophagus bending round the oesophagus, joining afterwards with the two uterine tubes. Tail slightly coiled, ending in a blunt, slightly swollen termination provided with irregular papilla-like projections. In some specimens where the tail end was

contracted the papillae were not conspicuous but the rugged and "shagreened" nature of the tip was clearly noticed.

Male. (After Chatterji, 1939). Length 90–100 mm., maximum diameter 0·5–0·6 mm. Muscular oesophagus 0·7–0·92 mm., glandular oesophagus 8·6–9·0 mm. Nerve ring at 0·24–0·26 mm. from anterior extremity. Tail 0·17–0·18 mm. long, loosely coiled spirally, ending in a pointed end and bearing eight pairs of caudal papillae: four pairs preanal, one pair adanal near the anterior lip of cloaca, and three postanal, the last three being situated more or less at equal distances from one another. Left spicule with a base 0·2–0·21 mm. long in the form of a stout curved tube to which is attached a distal slender part appearing to consist of two lash-like portions coiled with one another at certain points and ending in a membranous tip curved at an obtuse angle with the shaft; right spicule 0·12–0·14 mm. long, with thickly-studded spines around its external surface and bearing a dorsal gutter. The length of the filamentous portion of the left spicule has been a disputed point, Bernard and Bauche recording it as 0·07 mm. and Sandground as 0·15 mm. In the present material it was seldom found to be less than 0·22 mm., a length that exceeds the length of the basal portion of the spicule.

Type host : Domestic pig

Other hosts : *Sus cristatus*, Indian Wild Boar

Habitat : Peritoneal cavity

Type locality : Annam

Other localities : Burma

Discussion. See discussion under *Actionema congolensis*. As our material on this species is inadequate, we have reproduced a redescription of the parasite by Chatterji (1939) and his figure of the male tail.

ARTIONEMA ALTAICA (Raevskaya, 1928) n. comb.
(Figures 50–57)

Syns. and Litt.

Setaria altaica Raevskaya, 1928, pp. 25–30 (in *Cervus canadiensis asiaticus*, Altai-Shebalino, U.S.S.R.)

Setaria cervi Maplestone, 1931, pp. 92–4 (in *Cervus axis*, Calcutta Zoo, India)

Material. One male and three females from the Red Deer, *Cervus elaphus* from Ratibor hammer, Germany (Berlin Museum, No. 5128); five females from the Elk, *Alces alces*, Europe (Berlin Museum); one female from the Muntjac, *Muntiacus muntjak*, Namring, India (British Museum (Nat. Hist.)).

Description. The round mouth opening is surrounded by a prominent "slightly protruded" flat peribuccal crown. This peribuccal crown is oblong with its long axis dorso-ventral. It bears four large prominent elevations, about 40 microns apart ventrally, and 50 microns laterally. There are eight pairs of circumoral papillae and two lateral amphids. The diameter of the posterior oesophagus is roughly twice that of the anterior part.

Female. The female worm has a length of about 107–116 mm. and a maximum diameter of 0·9–1·1 mm. The oesophagus has a total length of 5·5–6·0 mm., the anterior part being 0·6–0·7 mm., the posterior part 4·9–5·3 mm. The nerve ring and cervical papillae are 0·27–0·29 mm. and 0·46–0·52 mm. respectively from the cephalic end. The vulva opens 0·4–0·47 mm. from the anterior end. The vagina, 7–8 mm. in length, proceeds caudally without coiling.

The posterior extremity of the worm is slightly coiled. The tail is about 0·5–0·6 mm. in length with the anal opening on the greater curvature. The tail ends in a spherical terminal knob like that of *Artionema digitata*. Laterally there are two large caudal appendages situated 0·05–0·06 mm. from the caudal extremity. These appendages are almost tubular and are not quite cone-shaped.

Male. The very much smaller male is about 47 mm. long and 0·51 mm. in maximum breadth. The total length of the oesophagus is 4·5 mm., the anterior part measuring 0·5 mm. and the posterior part 4·0 mm. The nerve ring and cephalic papillae are 0·27 mm. and 0·53 mm. respectively from the cephalic end. The caudal extremity ends in several coils. The tail is 0·19 mm. long, and has two large lateral caudal appendages. There is a single median precloacal papilla and eight paired lateral papillae, four pairs being precloacal and four postcloacal. These papillae in the other species are usually arranged in two straight rows and almost symmetrically placed; but occasionally in some specimens they are displaced in some other position. The second last papillae in the left row is often lateral and posterior, as it is with our present single male specimen from this host.

The curved right spicule has a length of 0.17 mm. The left spicule has its heavily sclerotized parts 0.36 mm. long, the pitted shaft is 0.21 mm. in length, and the blade 0.15 mm. The blade is covered by a long protruding sclerotized membrane.

Type host : *Cervus canadiensis asiaticus*

Other hosts : *Cervus elaphus*, *C. axis*, *Alces alces*, *Muntiacus muntjak*

Habitat : Peritoneal cavity

Type locality : Altai-Shebalino, U.S.S.R.

Other localities : Central Europe and India.

Discussion. A number of species of *Filaria* which have been reported from deer in Europe and Brazil probably belong to the genus *Artionema*. They are *Filaria cervi* Rudolphi, 1819 from *Cervus elaphus*, Europe; *Filaria cervina* Dujardin, 1845, from *Cervus elaphus*, Europe; *Filaria terebra* Diesing, 1851 from *Cervus elaphus*, Europe; *Filaria bidentata* Molin, 1858 from *Cervus nambi*, *C. simplicicornis* and *C. rufus*, from Brasil; and *Filaria cervi elaphi* Molin, 1858 from *Cervus elaphus* from Europe. The validity of these species has been the subject of a series of controversial papers none of which were conclusive. I have been informed by Dr. Kritscher of the Vienna Museum that these type specimens are no longer in their collection and are presumably lost.

In the absence of this material the logical procedure would be to examine specimens of *Artionema* from *Cervus elaphus* from various parts of Europe. I have now examined one collection of "Setaria" from *Cervus elaphus* from Ratibor hammer, Germany and found a species indistinguishable from the original description and drawings of *Setaria altaica* Raevskaya, 1928. In two further collections from deer in Germany, one in *Alces alces* and another in *Capreolus capreolus*, a mixed infection of two distinct species was present. One is *Artionema altaica* Raevskaya, 1928 whose type host and area are *Cervus canadiensis asiaticus* and Russia, respectively; the other is *Artionema hartwichi* n. sp. to be described later in this paper. It therefore appears that if more specimens were available from *Cervus elaphus* in Europe at least two or more species would be found.

The question therefore arises as to which of the two or more species involved is *Filaria cervi* Rudolphi, 1819 as seen by Rudolphi,

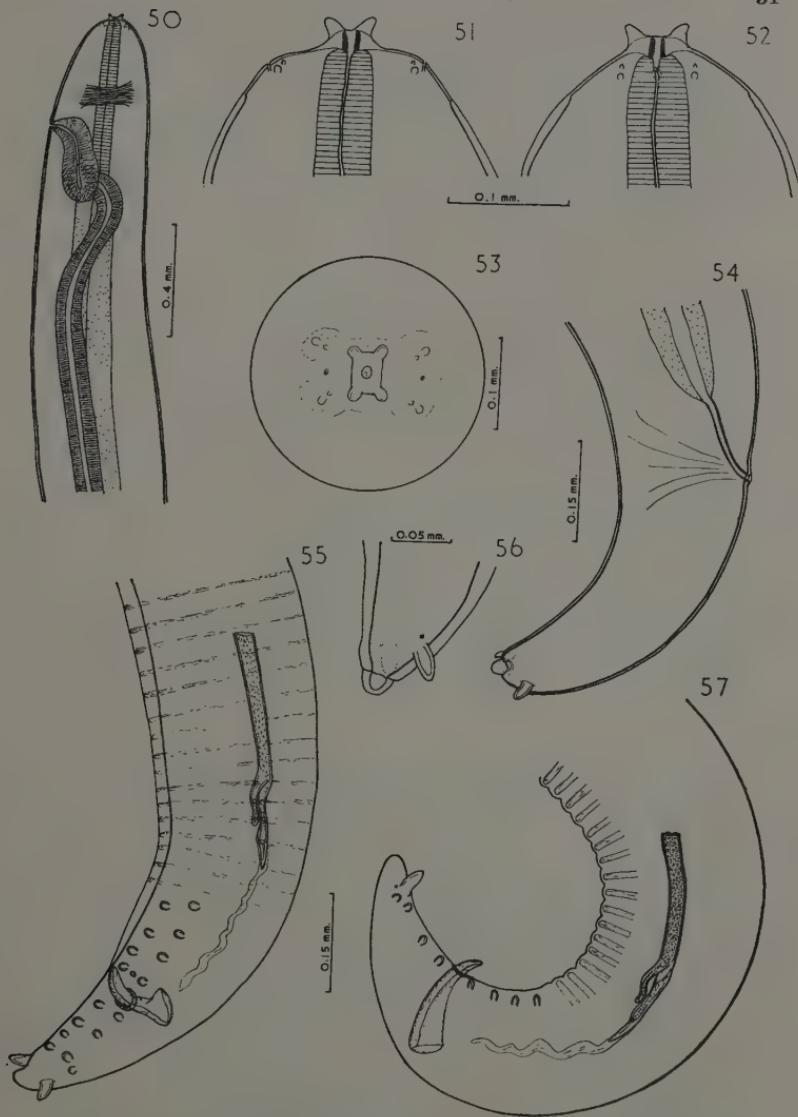
*Artionema altaica* (Raevskaya, 1928).

Fig. 50.—Anterior end of female worm. Fig. 51.—Ventral view of head. Fig. 52.—Lateral view of head. Fig. 53.—En face view. Fig. 54.—Female tail. Fig. 55.—Ventral view of male tail. Fig. 56.—Terminal part of female tail. Fig. 57.—Lateral view of male tail.

or were they a composite of two or more species? As the type specimens are lost, I propose, for the sake of stability in the nomenclature of the group, that the names *Filaria cervi* Rudolphi, 1819; *Filaria cervina* Dujardin, 1845; *Filaria terebra* Diesing, 1851; *Filaria bidentata* Molin, 1858 and *Filaria cervi elaphi* Molin, 1858 should be eliminated from the literature as *nomina dubia*, and unavailable for systematic purposes.

The final step would be to select from the literature the earliest available name in which the types are available or a recognizable description and drawing is given. The "*Setaria*" spp. from deer to be considered are in this order: *Setaria nudicauda* Ortlepp, 1924; *Setaria altaica* Raevskaya, 1928; *Setaria tundra* Isaichikov and Raevskaya, 1928; and *Setaria cervi* Maplestone, 1931.

Setaria nudicauda Ortlepp, 1924. This species was described on a single female specimen from "some species of deer" in Dutch Guiana, South America. The specimen is incomplete as the author says: "The peri-buccal cuticular ring is unfortunately incomplete, its ventral and lateral parts being absent. The remaining dorsal prominence of the peri-buccal ring is simple and not notched.... The anus is situated about 3 mm. from the posterior end. The tail which is smooth and loosely coiled, bears a pair of lateral papilla-like appendages at its tip. It tapers slightly but terminates in an obtuse tip."

I have examined the type specimen and found the peri-buccal crown to be incomplete and the tail certainly "*nudicauda*" as it is amputated across the caudal appendages and hence the appearance of the short terminal appendages and the obtuse tip as drawn by Ortlepp. It is surprising that the author did not notice the amputated tail. The species is therefore unidentifiable and I propose that this name be eradicated from systematic literature as a *nomen dubium*.

Setaria altaica Raevskaya, 1928. This species is well described and figured. Actually this paper (*Setarii i ikh patogennoe znachenie*) has excellent descriptions and drawings, and is probably the best review on the genus *Setaria* s.l. available. The author signed it August, 1927, Moscow. He added an addendum to include the new species described by Thwaite (1927). As this species is the earliest recognisable in the literature, I propose that this species be accepted as valid, even though one of the earlier poorly described species from the European deer, *Cervus elaphus*, might be conspecific.

Maplestone (1931) described a new species, *Setaria cervi* from *Cervus axis* in the Zoological Garden, Calcutta. This species is clearly conspecific with *A. altaica*, and is placed as a synonym by me.

Setaria tundra Isaichikov and Raevskaya, 1928. This is a good species. It is described, figured and discussed on the following pages.

ARTIONEMA HARTWICHI sp. nov.

(Figures 58-64)

Syn. and Litt.

Setaria tundra of Böhm and Supperer, 1955, pp. 166-8 (in *Capreolus capreolus*, Austria)

Material. One female specimen from the European Roe Deer, *Capreolus capreolus*, Europe (?Germany), (Berlin Museum Coll. No. Q3922); and one male specimen from the Elk, *Alces alces*, Europe (?Germany), (Berlin Museum Coll.).

Introduction. There is one recognisable description of this parasite in the literature. It was described as *Setaria tundra* by Böhm and Supperer, 1955. Their material was collected from *Capreolus capreolus* in Austria.

Description. The worm has a thick smooth cuticle. The mouth opening is round, the peribuccal crown is oblong with its long axis dorso-ventral, and are provided with two peribuccal elevations. These elevations are situated dorsally and ventrally 42 microns apart and are slightly bifid.

Female. The female has a length of 71 mm. and a maximum breadth of 0.64 mm. The oesophagus has a total length of 3.45 mm., the anterior part being 0.45 mm. and the posterior part 3.0 mm. The nerve ring is situated 0.2 mm. from the mouth. The vulva is 0.27 mm. from the cephalic end. The comparatively short vagina is 2.4 mm. in length.

The posterior extremity of the worm tapers very gradually and in the last few millimetres is very narrow. The very slender tail is 0.42 mm. in length. It terminates in a slightly elongated knob, and has two very small, lateral, inconspicuous, subterminal caudal appendages about 30 microns from the extremity.

Male. The male is 36 mm. long and 0·35 mm. in maximum breadth. The total length of the oesophagus is 2·85 mm., the anterior part is 0·45 mm. and the posterior part 2·4 mm. The nerve ring and cephalic papillae are 0·24 mm. and 0·49 mm. respectively from the cephalic end. The caudal extremity ends in several coils. The tail is 0·13 mm. in length, and has two small caudal appendages. The ventral surface has a number of transverse rugae. There is a single median precloacal papilla and eight paired papillae. Four pairs are precloacal and equally spaced, and the other four pairs are unevenly spaced with the last being lateral and posterior to the caudal appendage.

The spicules are comparatively short. The curved right spicule has a length of 0·06 mm. The left spicule has its heavily sclerotized parts 0·25 mm. long; the pitted shaft being 0·19 mm. in length and the blade only 0·06 mm. long. The short blade is enveloped by a long protruding sclerotized membrane.

Type host: *Capreolus capreolus*

Other hosts: *Alces alces*

Habitat: Peritoneal cavity

Type locality: Germany

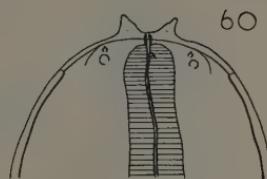
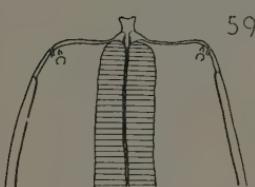
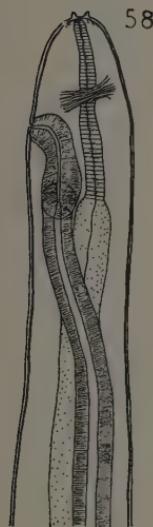
Other localities: Austria

This species is named in honour of Herrn Dr. G. Hartwich of the Zoologisches Museum der Humboldt-Universität zu Berlin.

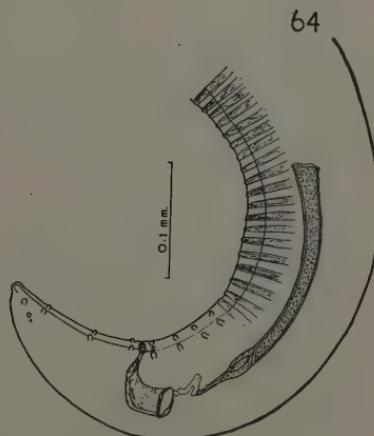
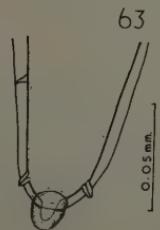
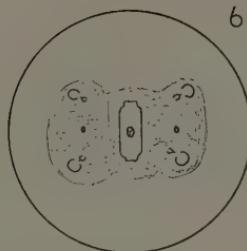
Discussion. See discussion under *Artionema altaica*. Böhm and Supperer (1955) erroneously described this species as *Setaria tundra*. This species differs from *S. tundra* in the female tail having very small subterminal appendages; these caudal appendages are large in *S. tundra* and further from the extremity. The female tail ends in a terminal knob, unlike *S. tundra*, in which it ends in a series of small knobs or spikes.

Artionema hartwichi sp. nov.

Fig. 58.—Anterior end of female worm. Fig. 59.—Ventral view of head. Fig. 60.—Lateral view of head. Fig. 61.—*En face* view. Fig. 62.—Female tail. Fig. 63.—Terminal part of female tail. Fig. 64.—Lateral view of male tail.



— 0.1 mm.



ARTIONEMA TUNDRA (Isaichikov and Raevskaya, 1928) n. comb.
(Figures 65-73)

Syn. and Litt.

Setaria tundra Isaichikov and Raevskaya, in Raevskaya, 1928, pp. 21-5. (In *Rangifer tarandus*, Arkhangelsk, U.S.S.R.)

Setaria tundra Isaichikov and Raevskaya, in Raevskaya, 1929, pp. 42-6. (German publication of above).

? *Setaria kabargi* Kadenzii, in Skrjabin and Shikhobalova, 1948, pp. 449-51. (In *Moschus moschiferus*, U.S.S.R.)

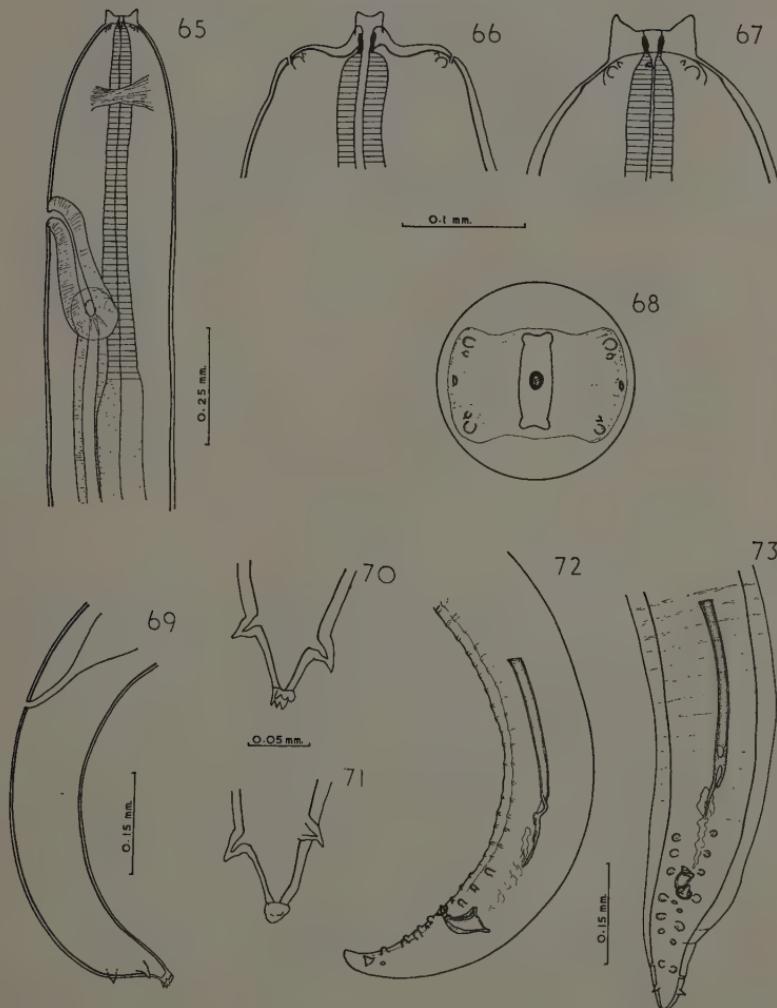
Material. Three male and three female specimens from *Odocoileus virginianus borealis*, from New Jersey, U.S.A., one male and one female specimen from *Odocoileus virginianus* (?) *nigribarbis*, from Ossabaw Island, Georgia, U.S.A., and one male and one female specimen from *Odocoileus hemionus columbianus*, from Northern California, U.S.A. (U.S. Dept. Agric. Coll., Beltsville).

Introduction. Three collections from North American deer were examined. They all belonged to *Artionema tundra*. The following description is based on four female and two male specimens.

Description. The round mouth opening has a marked buccal thickening, and is surrounded by a slightly raised peribuccal crown. The peribuccal crown is oblong with its long axis dorso-ventral, and are provided with two slightly bifid peribuccal elevations.

Female. The female has a length of 63-89 mm. and a maximum diameter of 0.53-0.62 mm. The dorso-ventral elevations are 54-67 microns apart. The oesophagus has a total length of 3.8-5.2 mm., the anterior being 0.5-0.7 mm. and the posterior part 3.3-4.5 mm. The nerve ring and cervical papillae are 0.19-0.27 mm. and 0.29-0.38 mm. respectively from the mouth. The vulva is 0.37-0.44 mm. from the cephalic end.

The posterior extremity of the worm tapers very gradually and becomes rather slender. The slender tail is 0.29-0.48 mm. in length and its diameter at the anus is 0.12 mm. The tail ends in a roughened knob which may be furnished with a number of spikes, and often looking very much like the tail of *Artionema labiato-papillosa*. The pair of large cone-shaped caudal appendages are 50-70 microns from the extremity.



Artionema tundra (Isaichikov and Raevskaya, 1928).

Fig. 65.—Anterior end of female worm. Fig. 66.—Ventral view of head. Fig. 67.—Lateral view of head. Fig. 68.—En face view. Fig. 69.—Lateral view of female tail. Figs. 70-1.—Terminal part of female tail. Fig. 72.—Lateral view of male tail. Fig. 73.—Ventral view of male tail.

Male. The male is 36–38 mm. long and 0·31 mm. in maximum breadth. The dorso-ventral elevations are 42–54 microns apart. The total length of the oesophagus is 3·1–3·5 mm., the anterior part is 0·5 mm. and the posterior part 2·6–3·0 mm. The nerve ring and cervical papillae are 0·18–0·21 mm. and 0·35 mm. respectively from the cephalic end. The tail is 0·15–0·18 mm. in length and are provided with two relatively large appendages 29 microns from the extremity. The ventral surface of the tail has a number of transverse rugae. There is a single median precloacal papilla and eight paired papillae.

The short spicule is 84 microns in length. The long spicule has its heavily sclerotized parts 0·33 mm. long ; the pitted handle is 0·23 mm. and the blade 0·1 mm. long.

Type host : *Rangifer tarandus*

Other hosts : *Moschus moschiferus*, *Odocoileus virginianus* and *O. hemionus*

Habitat : Peritoneal cavity

Type locality : Arkhangelsk, U.S.S.R.

Other localities : North America

Discussion. See discussion under *Artionema altaica*. This species has been wrongly reported many times in the literature as *S. cervi* and *S. labiato-papillosa*; and it appears that all North American records of these two species in Deer or Moose belongs to this species (Fenstermacher and Olsen, 1942; Olsen and Fenstermacher, 1942; and Erickson and Highby, 1942). This species is easy to differentiate from the cattle worm, *A. labiato-papillosa*. The cattle worm has an elongated mouth opening (visible from a lateral view) and cuticularized lateral lips, whereas *A. tundra* has a rounded mouth opening and no cuticularized lateral lips.

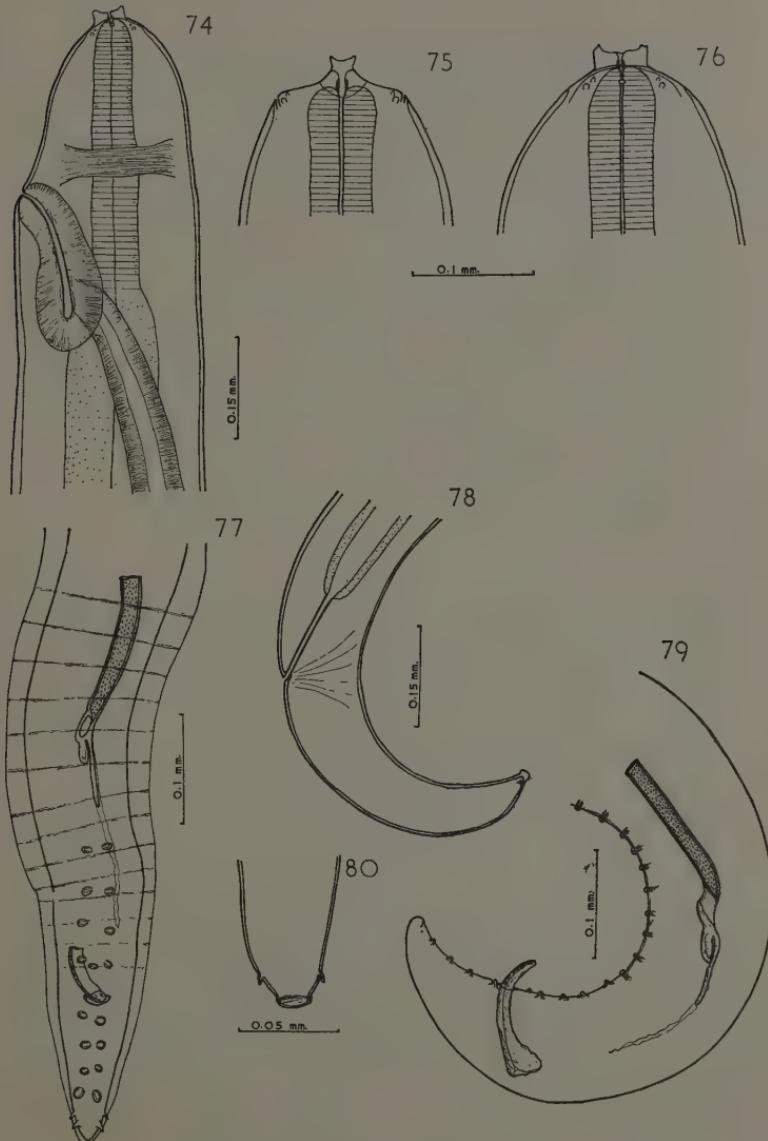
ARTIONEMA SCALPRUM (von Linstow, 1908) n. comb.

(Figures 74–80)

Syn. and Litt.

Filaria scalprum von Linstow, 1907, p. 26.

Material. Type material consisting of one female and one male and a number of damaged or fragmented specimens from the Steinbok, *Raphicerus campestris*, Kalahari, Africa. (Zool. Mus. Berlin, No. 4724).



Artionema scalprum (von Linstow, 1908).

Fig. 74.—Anterior end of female worm. Fig. 75.—Ventral view of head. Fig. 76.—Lateral view of head. Fig. 77.—Ventral view of male tail. Fig. 78.—Lateral view of female tail. Fig. 79.—Lateral view of male tail. Fig. 80.—Terminal part of female tail.

Two females and one male from type host, Grahamstown, S. Africa; eight females and six males from the Impala, *Aepyceros melampus*, Machili, N. Rhodesia (P. L. LeRoux Coll.). One female and one male from the gazelle, *Gazella granti*, Uganda; three females and one male from *G. granti*, Uganda; two females and three males from Oribi, *Ourebia kenyae* from Uganda; seven females and one male from *O. kenyae*, Uganda. (Brit. Mus. Coll.).

Introduction. This species was briefly described by von Linstow (1908), but his description and figures are not sufficient by modern standards. We have chosen to give the measurements and description with figures of a pair of undamaged types.

Description. The round mouth opening is surrounded by a slightly protruded peribuccal crown which is provided with a dorsal and a ventral bifid peribuccal elevation. The division of the oesophagus in two parts is not quite so distinct as in most of the other species. The anterior tip of the oesophagus is straight when viewed laterally, but on the dorsal or ventral aspect, it is slightly swollen.

Female. The female measures 95 mm. in length with a maximum width of 0·67 mm. The oesophagus is comparatively short, the total length being only 5·12 mm., its anterior part measuring 0·42 mm. and the posterior part 4·7 mm. The nerve ring is 0·17 mm. from the cephalic end. The vulval opening is a vertical slit, 0·29 mm. from the mouth. The tail is 0·42 mm. long and generally ends in a small knob often ill-defined. Lateral to this knob and only 0·02 mm. from the caudal extremity are a pair of small appendages. The anterior part of the worm is much distended with microfilariae.

Male. The male is a very much smaller worm, only 37 mm. in length with a maximum breadth of 0·27 mm. The oesophagus has a total length of 3·92 mm., the anterior portion measuring 0·38 mm. and the posterior part 3·54 mm. The nerve ring is 0·21 mm. from the cephalic end. The short tail is 0·12 mm. long. There are eight paired caudal papillae, four precloacal and four postcloacal. In addition to this, there is also a single median precloacal papilla and a pair of small subterminal lateral appendages. The broad, right spicule measures 0·13 mm. in length. The left spicule has a pitted shaft 0·14 mm. long and a blade 0·10 mm., a total length of 0·24 mm.

Type host : *Raphicerus campestris*, Steinbok

Other hosts : *Aepyceros melampus* (Impala), *Gazella granti* (Gazelle) and *Ourebia kenyae* (Oribi).

Habitat : Peritoneal cavity

Type locality : Kalahari (zw. Kooa ü. Segkoma), Africa.

Other localities : South Africa, Northern Rhodesia and Uganda

Discussion. The above records from the Impala, Gazelle and Oribi are all new host records. This species, *Artionema scalprum* (von Linstow, 1908) has often been identified with *Artionema bicoronata* (von Linstow, 1901) under the name *Setaria hornbyi* Boulenger, 1921 by most contemporary workers. The two species, however, are quite distinct from one another. *A. scalprum* has a relatively short oesophagus and a pair of small caudal appendages very close to the terminal knob. The paired caudal appendages are much smaller than those found in *A. bicoronata* and also much closer to the terminal knob. A careful examination will show the three above mentioned species are quite distinct and should not be confused with one another.

ARTIONEMA CAELUM (von Linstow, 1904) n. comb.

(Figures 81-89)

Syns. and Litt.

Filaria cornuta von Linstow, 1899, p. 24 (in *Antilope* sp. Edea, Cameroons, W. Africa).

Filaria caelum von Linstow, 1904, pp. 299-300 (in *Cephalophus sylviculator*, Cameroons, W. Africa).

Filaria transversata von Linstow, 1907, p. 258 (in *Cephalophus melanorheus*, Bipindi, Cameroons, W. Africa).

Setaria cornuta of Boulenger, 1928, pp. 38-9 (in *Cephalophus monticola*, W. Africa).

Setaria sandersoni Baylis, 1936, pp. 267-71 (in *Philantomba melanorhea*, Cameroons, W. Africa).

Material. *Type material* (*Filaria caelum*). Two males and one female and a fragmented female from *Cephalophus sylviculator*, Cameroons, W. Africa. (No. 51, Evertebratavdelningen, Naturhistoriska Riksmuseet, Stockholm).

Type material (*Filaria cornuta*). One male and fragmented females from *Antilope* sp. Edea, Cameroons, W. Africa. (Nr. 3755 Zoologischen Museums in Berlin).

Type material (*Filaria transversata*). One male and one female plus a number of fragmented females from *Cephalophus melanorheus*, Cameroons, W. Africa. (Nr. 4244 Zool. Mus. Berlin).

Type material (Setaria sandersoni). One male and seven females from *Philantomba melanorhea*, Cameroons, W. Africa. (No. 158, British Museum (Nat. Hist.)).

Twenty-five females and one male from eight Duikers, *Cephalophus maxwelli* and *C. dorsalis* from W. Africa (Died in London Zoo. L.S.H.T.M. Coll.) One female and two males from two Duikers, Nteko, N. Rhodesia (P. L. LeRoux Coll.).

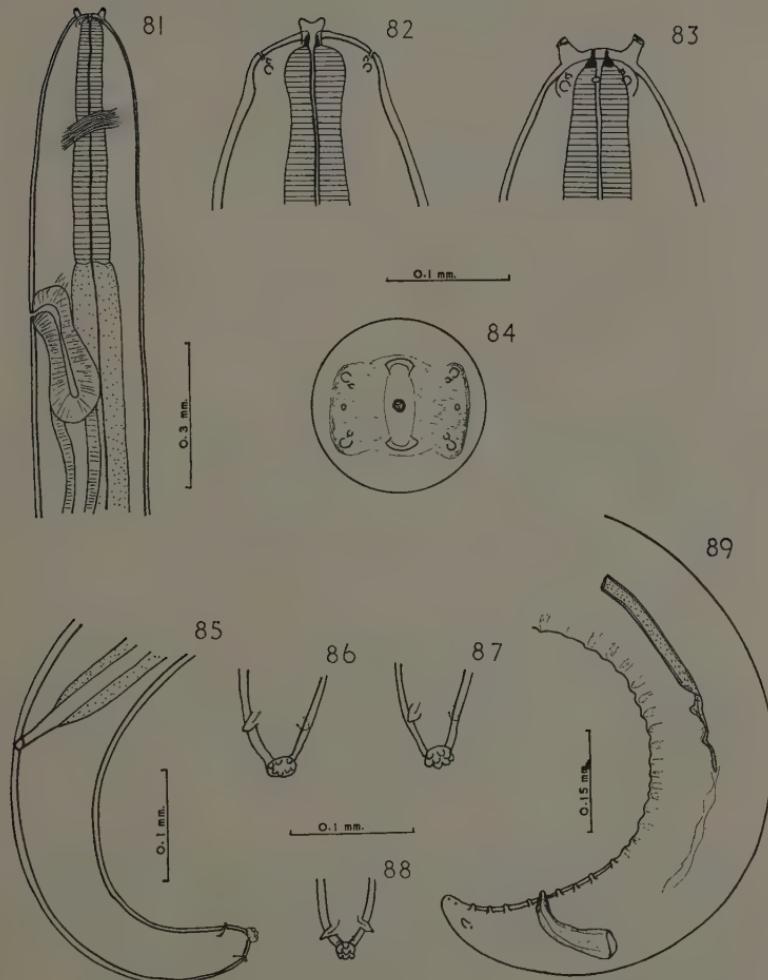
Introduction. It appears that this species has only once been correctly reported in the literature (Boulenger, 1928). It is not surprising that other records are incorrect as the original descriptions are insufficient by modern standards. The following redescription is made from the one female and two male types in the Stockholm Museum.

Description. The worm has a thin smooth cuticle. The round mouth opening is surrounded by a peribuccal crown which is oblong with its long axis dorso-ventral. The peribuccal ring is provided with two peribuccal elevations about 90 microns apart. These elevations are only slightly bifid and in slightly contracted specimens the free ends are often bent towards the mouth. In such cases the mouth appears to be hidden by the lateral shoulders of the worm.

Female. The female has a length of 124 mm. and a maximum breadth of 0.85 mm. The total length of the oesophagus is 18.9 mm., the anterior part measuring 0.9 mm. and the posterior measuring 18 mm. The nerve ring and cervical papillae are 0.35 mm. and 0.39 mm. respectively from the mouth. The vulval opening is 0.35 mm. from the cephalic end.

The anus is 0.5 mm. from the extremity. The diameter of the tail across the anus is 0.14 mm. The tail terminates in a depressed knob which commonly consists of a number of small lobes. Close-by there are two small lateral appendages, about 40 microns from the extremity.

Male. The male is 68-70 mm. long and 0.45 mm. in maximum breadth. The total length of the oesophagus is 17.5-20.4 mm., the anterior part measuring 0.4-0.5 mm. and the posterior part 17-20 mm. The nerve ring and cephalic papillae are 0.2 mm. and 0.4 mm. respectively from the cephalic end. The caudal extremity ends in one or two coils. The tail is 0.13-0.14 mm. long, and has two small, rather inconspicuous caudal appendages about 40 microns from the extremity. The ventral surface of the posterior end has a number



Artionema caelum (von Linstow, 1904).

Fig. 81.—Anterior end of female worm. Fig. 82.—Ventral view of head. Fig. 83.—Lateral view of head. Fig. 84.—En face view. Fig. 85.—Female tail. Figs. 86–8.—Terminal part of female tail. Fig. 89.—Lateral view of male tail. (All figures drawn from type specimens).

of transverse rugae. There is a single median precloacal papilla and eight paired papillae. Four pairs are precloacal and four pairs postcloacal. At the extreme tip of the tail there are in addition two pairs of very minute papillae.

The curved right spicule has a length of 0·15–0·17 mm. and has ridges on its distal extremity. The left spicule has its heavily sclerotized parts 0·29–0·35 mm. long, the pitted shaft is 0·19–0·21 mm. in length, while the blade is 0·10–0·14 mm. long.

Type host : *Cephalophus sylviculator*, duiker

Other hosts : *C. dorsalis*, *C. maxwelli*, and *C. melanorheus*.

Habitat : Peritoneal cavity

Type locality : Cameroons, W. Africa

Other localities : Southern Africa

Discussion. There are four described species that are conspecific. I have chosen *Artionema caelum* as type because both male and female type specimens are available and in good condition, and the host is known. *A. caelum* was chosen rather than the senior member, *F. cornuta*, of which only one complete male is available, in poor condition, and the host is an unknown species of antelope.

It is rather surprising that von Linstow described the same species as new several times. Boulenger (1928) probably working by host and locality correctly identified this species. Baylis (1936) described *Setaria sandersoni* as a new species and mentioned that it might be conspecific with *F. cornuta*, but as the original description of *F. cornuta* is inadequate, he preferred to name his specimens as new. From the type specimens available I am satisfied that they are synonymous.

von Linstow (1907) in describing *F. transversata* lists both *Cephalophus melanorheus* and *Troglodytes niger* as hosts. I was not able to examine specimens from his latter host, but believe it is very unlikely that they belong to *Artionema*. It is also of interest to note that in the various new species described in this group by von Linstow, he failed to see the long left spicule each time, and duplicated the short right spicule in every instance.

I refrain from listing under synonyms and literature any doubtful records which cannot be checked, or records consisting of composite species such as those of Mönnig (1924), Thwaite (1927), van den Berghe and Vuylsteke (1936) and others.

ARTIONEMA DIPETALONEMATOIDES
(Chabaud and Rousselot, 1956) n. comb.
(Figures 90-97)

Syn. and Litt.

Setaria dipetalonematooides Chabaud and Rousselot, 1956,
pp. 70-4 (in *Guevei coeruleus*, Brazzaville, Congo)

Material. Five males and six females from *Cephalophus monticola* (= *Guevei coeruleus*), type host, West Africa; two males and six females from *Cephalophus maxwelli*, West Africa; and a number of specimens in poor condition from a Duiker, W. Africa. (All collected from animals dying at the London Zoo, L.S.H.T.M. Coll.).

Introduction. The material from *Cephalophus monticola* was collected from the London Zoo in 1948 and determined by Prof. Buckley as *Setaria* n. sp. and left undescribed in the School collection. Chabaud and Rousselot (1956) rightly recognized it as an undescribed species and gave a good account of the parasite. Their material was collected from the intermuscular connective tissue, and consisted of one male and a number of females in various conditions.

Description. This is a rather smallish worm with a very thick cuticle. The round mouth opening has a small buccal capsule. The mouth is surrounded by a characteristic peribuccal crown with a dorsal and a ventral undivided peribuccal elevation. In lateral view the elevations are pointed and cone-like; in ventral view they have a smooth blunt square edge.

Female. The female worm has a length of 65-74 mm. and a maximum breadth of 0.35-0.45 mm. The dorsal and ventral elevations are 50-65 microns apart. The oesophagus has a total length of 9-11 mm., the anterior part measures 0.4-0.5 mm. and the posterior part 8.5-10.5 mm. The nerve ring and cervical papillae are 0.2-0.3 mm. and 0.3-0.4 mm. respectively from the cephalic end. The vulval opening is 0.2-0.3 mm. from the mouth. The rather slender tail has a length of 0.6-0.65 mm. with the anus on the convex surface of its curvature. The diameter of the tail at the anus is 0.1-0.12 mm. The tail ends in a small spherical knob. There is a pair of comparatively small caudal appendages 40-50 microns from the extremity.

Male. The male has a length of 34–40 mm. and a maximum breadth of 0·2–0·3 mm. The dorsal and ventral elevations are 38–46 microns apart. The oesophagus has a total length of 7–11 mm., the anterior portion measuring 0·3–0·5 mm. and the posterior part 6·5–10·5 mm. The nerve ring and cervical papillae are 0·2–0·25 mm. and 0·3–0·4 mm. respectively from the cephalic end. The tail is slender, 0·16–0·20 mm. in length. The ventral precloacal surface has a large number of transverse rugae. There is a single median precloacal papilla, four pairs of precloacal papillae and four pairs of postcloacal papillae. As in the other species, there are always one or two pairs of very small inconspicuous subterminal papillae. There is a pair of small caudal appendages about 30–40 microns from the extremity, and a short distance anterior to them are the paired phasmids. The right spicule measures 0·11–0·13 mm. in length. The left spicule has a shaft 0·19–0·21 mm. and a blade of 0·13 mm.

Type host : *Cephalophus monticola*, duiker

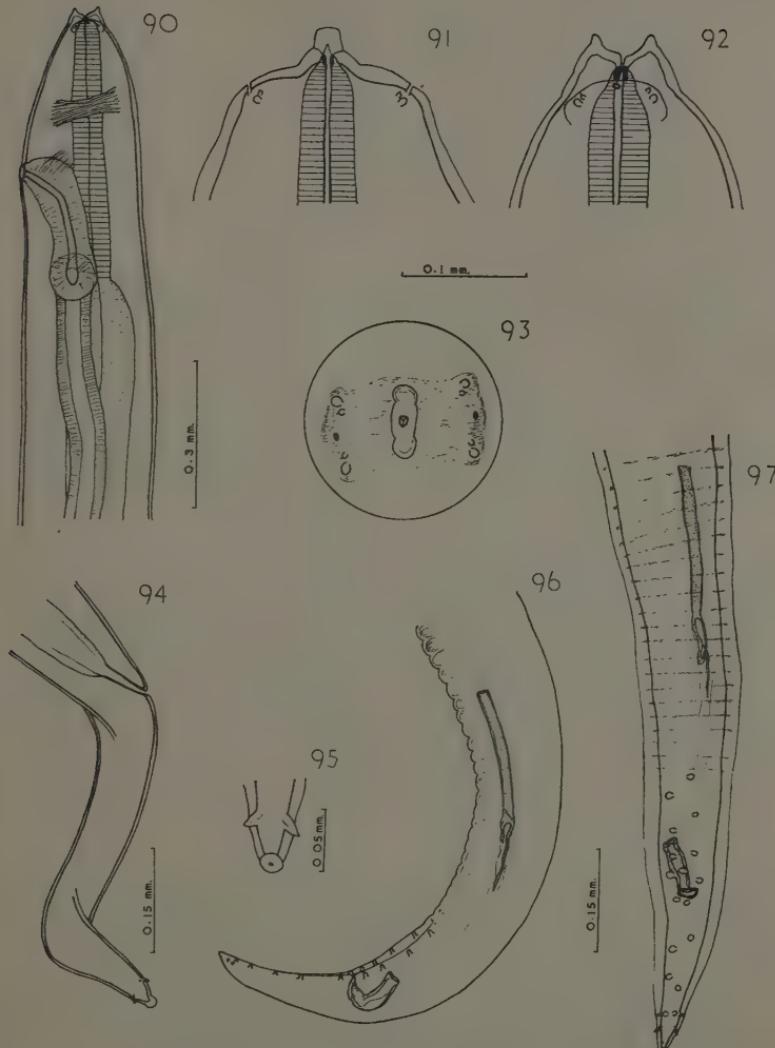
Other host : *C. maxwelli*

Habitat : Mainly peritoneal cavity

Type locality : Brazzaville, Congo

Other localities : West Africa

Discussion. The finding of this parasite in *Cephalophus maxwelli* is a new host record. The present specimens from the type host resemble the drawings of Chabaud and Rousselot (1956) very well in that the peribuccal crown is slightly contracted into the body. In the specimens from *Cephalophus maxwelli* they are well "protruded" or relaxed. I do not attach much significance to this fact however as it is almost certainly due to preservation methods, and am quite happy that they are conspecific. In a ventral view, the edge of the peribuccal elevation is square and not cone-like as shown by Chabaud and Rousselot. In their specimens presumably this structure is slightly eroded, a common occurrence in this genus.



Artionema dipetalonematooides (Chabaud and Rousselot, 1956).

Fig. 90.—Anterior end of female worm. Fig. 91.—Ventral view of head. Fig. 92.—Lateral view of head. Fig. 93.—En face view. Fig. 94.—Female tail. Fig. 95.—Terminal part of female tail. Fig. 96.—Lateral view of male tail. Fig. 97.—Ventral view of male tail.

ARTIONEMA SOUTHWELLI (Thwaite, 1927) n. comb.
(Figures 98–106)

Syns. and Litt.

Setaria southwelli Thwaite, 1927, pp. 448–51 (in *Cephalophus* sp., Sierra Leone, West Africa)

Setaria southwelli of Baylis, 1936, pp. 267–71 (re-examined types)

Material. Type material consisting of eighteen males and twenty-five females from *Cephalophus* sp. Sierra Leone, W. Africa. (Liverpool School of Tropical Medicine Coll.) and Cotype consisting of one male and one female (British Museum Coll.)

Description. The worm has a smooth cuticle. The round mouth opening has a small buccal capsule, and is surrounded by a peribuccal crown which has a dorsal and a ventral elevation. Each elevation is tooth-like, or rather like a stout cone with a heavy base.

Female. The female has a length of 96–110 mm. and a maximum breadth of 0·4–0·7 mm. The dorsal and ventral elevations are 66–80 microns apart. The oesophagus has a total length of 14·6–16·6 mm., the anterior part measuring 0·5–0·6 mm. and the posterior part 14·1–16·0 mm. The nerve ring and cervical papillae are 0·22–0·27 mm. and 0·43–0·63 mm. respectively from the cephalic end. The vulval opening is 0·44–0·55 mm. from the mouth. The tail has a length of 0·31–0·44 mm. and a diameter at the anus of 0·1–0·13 mm. The tail ends in a button-like knob with a few small blunt spines. The caudal appendages are relatively small, 30–50 microns from the extremity.

Male. The male has a length of 51–58 mm. and a maximum diameter of 0·29–0·35 mm. The dorsal and ventral elevations are 55 microns apart. The oesophagus has a total length of 11·5–12·8 mm., the anterior part measuring 0·5–0·6 mm. and the posterior part 11·0–12·3 mm. The nerve ring and cervical papillae are 0·19–0·24 mm. and 0·4–0·54 mm. respectively from the cephalic end. The tail is rather short and ends abruptly, thereby giving it a short fleshy appearance. It is 0·11–0·13 mm. in length. The ventral precloacal surface has a large number of weak transverse rugae. There is a single median precloacal papilla, four paired precloacal papillae and another four paired postcloacal papillae. The paired caudal appendages are relatively small and papilla-like. Posterior

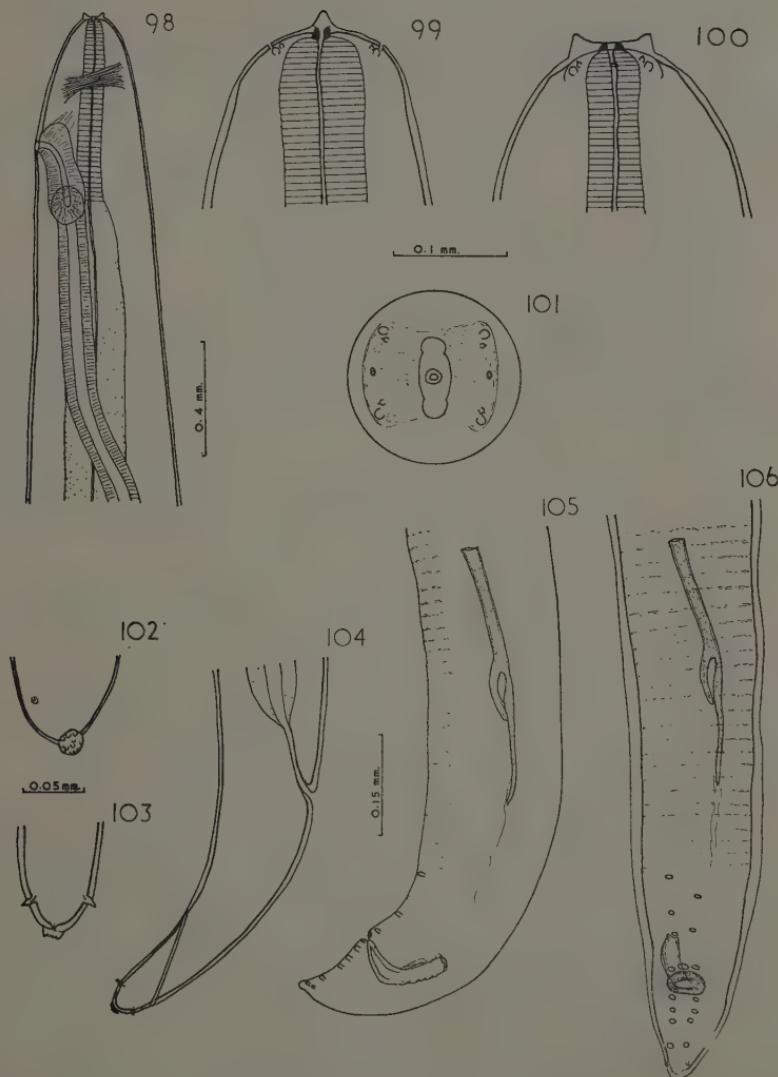
*Artionema southwelli* (Thwaite, 1927).

Fig. 98.—Anterior end of female worm. Fig. 99.—Ventral view of head. Fig. 100.—Lateral view of head. Fig. 101.—En face view. Figs. 102-3.—Terminal part of female tail. Fig. 104.—Female tail. Fig. 105.—Lateral view of male tail. Fig. 106.—Ventral view of male tail. (All figures drawn from type specimens).

to the appendages are two pairs of minute papillae. The cloacal opening is transversely elongated and cuticularized. The strongly curved right spicule is 0·15–0·18 mm. in length. The left spicule has a lightly pitted shaft 0·19–0·21 mm. in length and a blade of 0·15–0·18 mm.

Type host : *Cephalophus* sp. (On the cotypes is written "Black duiker" =? *Cephalophus nigrifrons*)

Habitat : Mainly peritoneal cavity

Type locality : Sierra Leone, West Africa.

Discussion. Although I have examined a number of *Cephalophus* spp. from West Africa, I have not found this species again, and am rather doubtful of its validity. As the type material appears to be normal, I accept the species tentatively unless further material proves it to be otherwise.

ARTIONEMA HORNBYI (Boulenger, 1921) n. comb.

(Figures 107–114)

Syns. and Litt.

Setaria hornbyi Boulenger, 1921, pp. 347–9 (in *Hippotragus niger*, Northern Rhodesia)

Setaria hornbyi of Vevers, 1923, p. 918 (in *Hippotragus equinus*, London Zoo)

Setaria thwaitei Mönnig, 1933, pp. 21–3 (in *Hippotragus niger*, *H. equinus* and *Cobus ellipsiprymnus*, Transvaal, South Africa)

Setaria hornbyi var. *brevicaudatus* Kreis, 1938, pp. 103–5 (in *Hippotragus* sp. Angola)

Material. One male and one female from *Hippotragus niger*, N. Rhodesia; three females from *H. equinus*, one female from *H. equinus*, twenty-seven females and twelve males from *H. equinus*, N. Rhodesia; one female from *Alcelaphus lichtensteini*, and four females and one male from *A. lichtensteini*, N. Rhodesia (P. L. LeRoux Coll.). Two females from *H. equinus* and seven females and two males from *H. equinus*. (L.S.H.T.M. Coll.).

Introduction. The name of this parasite is very common in the literature, but unfortunately most of the identifications are incorrect. The above list of synonyms and literature are therefore restricted mainly to records of so-called new species. The extensive records are omitted because they are either incorrectly determined or consist of composite species.

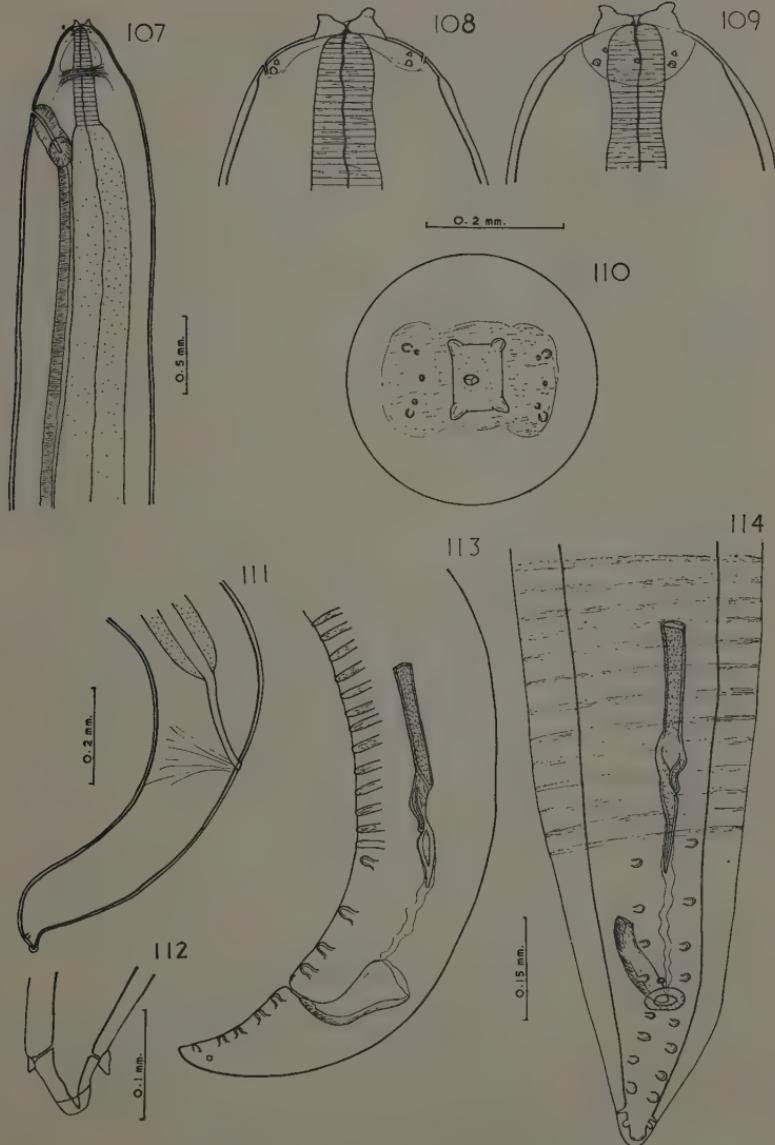
*Artionema hornbyi* (Boulenger, 1921).

Fig. 107.—Anterior end of female worm. Fig. 108.—Ventral view of head. Fig. 109.—Lateral view of head. Fig. 110.—En face view. Fig. 111.—Lateral view of female tail. Fig. 112.—Terminal part of female tail. Fig. 113.—Lateral view of male tail. Fig. 114.—Ventral view of male tail.

Description. This worm is one of the largest species in the genus. Its length and diameter reaches about twice that of most of the other species. The body cuticle is thick and smooth. The round mouth opening has a peribuccal crown with four elevations which are symmetrically placed and far apart.

Female. The female is a very large worm, measuring 155–215 mm. in length and a maximum breadth of 1·2–1·5 mm. The oesophagus has a total length of 13·8–18·3 mm., the anterior part measuring 0·7–0·9 mm. and the posterior part 13–18 mm. The nerve ring and cervical papillae are 0·26–0·35 mm. and 0·69–0·76 mm. respectively from the cephalic end. The vulval opening is 0·46–0·62 mm. from the mouth. The ovejector is large, and the vagina runs posteriad without coiling. The tail has a length of 0·40–0·69 mm. and ends in a small terminal knob. The paired caudal appendages are 0·06–0·08 mm. from the caudal extremity. The uterus is filled with microfilariae.

Male. The male has a length of 56–80 mm. and a maximum breadth of 0·54–0·62 mm. The oesophagus has a total length of 10–16 mm., the anterior part measuring 0·40–0·51 mm. and the posterior part 9·8–15·6 mm. The nerve ring is 0·25–0·29 mm. from the cephalic end. The tail is 0·18–0·21 mm. long. The caudal alae are well developed for about 15 mm. and the same length of which is covered on the ventral surface with transverse cuticular rugae. When viewed laterally, these rugae appear very much like small papillae, but closer examination show them to traverse the entire ventral surface and disappear under the cuticle laterally. There is a single median precloacal papilla, and eight pairs of large caudal papillae of which four pairs are precloacal and four postcloacal. As in the other species there are a number of smaller papillae on the tip of the tail, and in this instance, at least one pair is of fair size. The lateral caudal appendages are small. The right spicule has a length of 0·17–0·20 mm. The left spicule has its heavily sclerotized parts 0·33–0·43 mm. long, the shaft measuring 0·20–0·23 mm. and the blade 0·13–0·19 mm.

Type host : *Hippotragus niger*, Sable Antelope

Other hosts : *H. equinus*, *Alcelaphus lichtensteini* and ?*Cobus ellipsiprymnus*. Various doubtful records in the literature are not listed here

Habitat : Peritoneal cavity

Type locality : Northern Rhodesia

Other localities : S. Africa, N. Rhodesia, East Africa, Sudan, Congo and Angola.

Discussion. This parasite was first collected by H. E. Hornby from the Sable Antelope, *Hippotragus niger* in Northern Rhodesia and adequately described and figured by Boulenger (1921). Boulenger also states that "Mr. Hornby writes that he has seen similar forms parasitic in the Eland, Water-Buck and Reed-Buck." From my studies of *Artionema* spp. in the above-mentioned animals in Northern Rhodesia, I believe it is quite safe to dismiss them as not being *A. hornbyi*, and to take "similar forms" as meaning *Artionema* spp. Two years after the appearance of Boulenger's paper, Vevers (1923) recorded *A. hornbyi* from a related host, the Roan Antelope, *Hippotragus equinus* which died in the London Zoo. Then Thwaite (1927) published his work on the genus *Setaria* which soon became the standard work of reference on the subject. Thwaite gave a detailed redescription and drawings of the species to show the great range of variation in the species. Unfortunately he was not dealing with *A. hornbyi* (Boulenger, 1921) but a heterogeneous collection of several species of *Artionema*. Mönnig (1933) when he found the true *Artionema hornbyi* which Boulenger described, took the trouble to name it *Setaria thwaitei* new species, with his only cited reference being Thwaite (1927). Since then and right up to date, this heterogeneous collection of *Artionema* spp. have consistently been identified as *Setaria hornbyi* Boulenger, 1921 in the literature, and the true *A. hornbyi* have often been identified as *Setaria thwaitei*—a very serious mistake which has not been noticed earlier. It is not clear how Thwaite could have made such a blunder as the size of the worm alone was sufficient to separate them. *A. hornbyi* is much larger than the other species concerned. Moreover the head end is very distinctive.

ARTIONEMA BICORONATA (von Linstow, 1901) n. comb.
(Figures 115–122)

Syn. and Litt.

Filaria bicoronata von Linstow, 1901, p. 411 (in *Adenota loderi*, Lake Rukwa, Tanganyika Territory)

Material. Type material consisting of a single female specimen broken in two, otherwise in reasonable condition. Collected by Prof. Fülleborn from *Adenota loderi*, Lake Rukwa, Tanganyika Territory. (Nr. 4020, Zool. Mus. Berlin).

Also an extensive collection of well over 100 male and female specimens from *Kobus leche*, *K. vardoni*, "Waterbuck" and the Reedbuck, *Redunca arundinum* from Portuguese East Africa,

Northern Rhodesia and Nyasaland (L.S.H.T.M. Coll. and P. L. LeRoux Coll.).

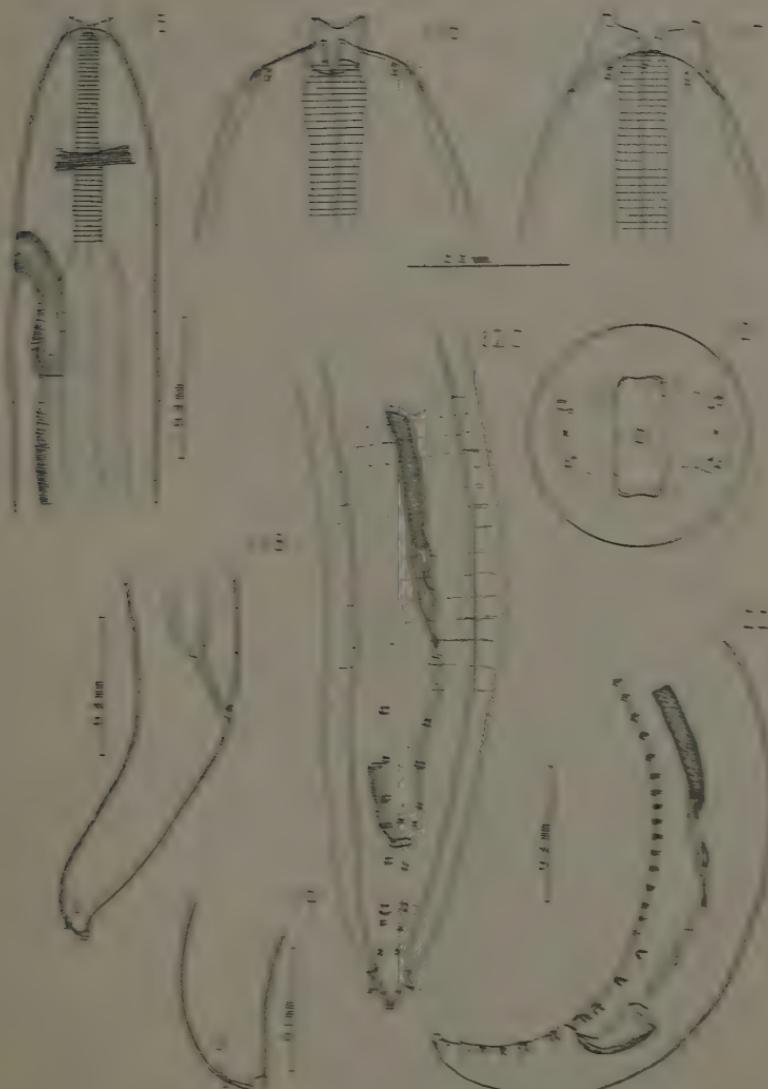
Introduction. As this species was poorly described by von Linstow, further records of it did not appear in the literature. I propose to give a very brief redescription of the single female type and then give a more detailed redescription of the species from other material from a related host, *Kobus leche*.

Redescription of female type specimen. The worm measures 62.5 mm. in length and 0.6 mm. in maximum breadth. The mouth has a small buccal capsule and is surrounded by a prominent peri-buccal crown. The peribuccal elevations are bifid. The oesophagus has a total length of 6.2 mm. with the anterior muscular part 0.5 mm. and the posterior part 5.7 mm. in length. The nerve ring and cervical papillae are 0.29 mm. and 0.59 mm. respectively from the cephalic end. The vulva opens 0.48 mm. from the mouth. The lightly coiled tail is 0.41 mm. long. The tip of the tail ends in a single roughened knob. Lateral to this knob are the paired caudal appendages, 0.05 mm. from the tip of the tail.

Redescription from Kobus leche material

Female. The female measures 97–116 mm. in length with a maximum breadth of 0.6–0.7 mm. The dorsal and ventral elevations are 0.11–0.13 mm. apart. The oesophagus has a length of 8.3–9.6 mm., the anterior part measuring 0.5–0.7 mm. and the posterior part 7.7–8.9 mm. The nerve ring and cervical papillae are 0.27–0.30 mm. and 0.4–0.5 mm. respectively from the cephalic end. The vulval opening is 0.34–0.42 mm. from the mouth. The tail measures 0.6–0.75 mm. in length. The tail has a terminal knob or quite often a truncated terminal knob resembling a finger thimble with the truncated end slightly indented. Lateral to this are two large appendages 0.07–0.08 mm. from the caudal extremity.

Male. The male has a length of 48–51 mm. and a maximum breadth of 0.36–0.38 mm. The dorsal and ventral elevations are about 0.08 mm. apart. The oesophagus has a total length of 6.5–8.0 mm., the anterior part measuring 0.5–0.6 mm. and the posterior part 6.0–7.4 mm. The nerve ring and cervical papillae are 0.23–0.27 mm. and 0.38–0.42 mm. respectively from the cephalic end. The tail is 0.21–0.22 mm. long. There is a single median precloacal papilla and eight paired caudal papillae, four precloacal and four



Amphorina longistriata sp. n. Linsenw. 1940

Fig. 115.—Anterior end of female worm. Fig. 116.—Ventral view of head. Fig. 117.—Lateral view of head. Fig. 118.—Female tail. Fig. 119.—Dorsal view of male tail. Fig. 120.—Dorsal view of male tail. Fig. 121.—End-on view. Figs. 115-19 are drawn from type specimen.

postcloacal. In addition there can be seen one or two very minute pairs of subterminal caudal papillae. The curved right spicule measures 0·15–0·16 mm. in length. The left spicule has a shaft 0·18–0·19 mm. long and a blade 0·14–0·15 mm. The blade is enveloped by a long protruding sclerotized membrane.

Type host : *Adenota loderi*

Other hosts : *Kobus leche*, *K. vardoni* and *Redunca arundinum*

Habitat : Peritoneal cavity

Type locality : Lake Rukwa, Tanganyika Territory

Other localities : Mozambique, N. Rhodesia and Nyasaland

Discussion. von Linstow's brief description and drawing were inadequate to identify this species. He made only a single drawing of the worm, an anterior view of the head which was unfortunately not very accurate. The view of his specimen was neither lateral nor ventral, hence the appearance of the peribuccal elevations was incorrect and deceptive. What he drew as two cephalic spikes were in fact the outer borders of the "raised shoulders" which are typical when viewed in that position. It was possible to reproduce that view both with the type and with present specimens.

Yeh (1958b) has shown that this species has erroneously been reported many times in the literature under the name *Setaria hornbyi* Boulenger, 1921. This confusion is mainly due to Mönnig (1924) and Thwaite (1927) who redescribed what they believed to be *Artionema hornbyi*, but unfortunately, according to my observations, they were dealing with more than one species and probably no material of *Artionema hornbyi*. All authors who followed the work of Thwaite incorrectly identified *A. hornbyi*, but continued to identify his composite species.

The present records from *Kobus leche*, *K. vardoni* and *Redunca arundinum* are all new host records.

ARTIONEMA BOULENGERI (Thwaite, 1927) n. comb.
(Figures 123–131)

Syns. and Litt.

Setaria boulengeri Thwaite, 1927, pp. 451–2 (in *Redunca fulvorufula*, Rustenberg, Transvaal, S. Africa)

Material. Type material consisting of two females from *Redunca fulvorufula*, Transvaal, S. Africa. (Liverpool School of Tropical Medicine Coll.).

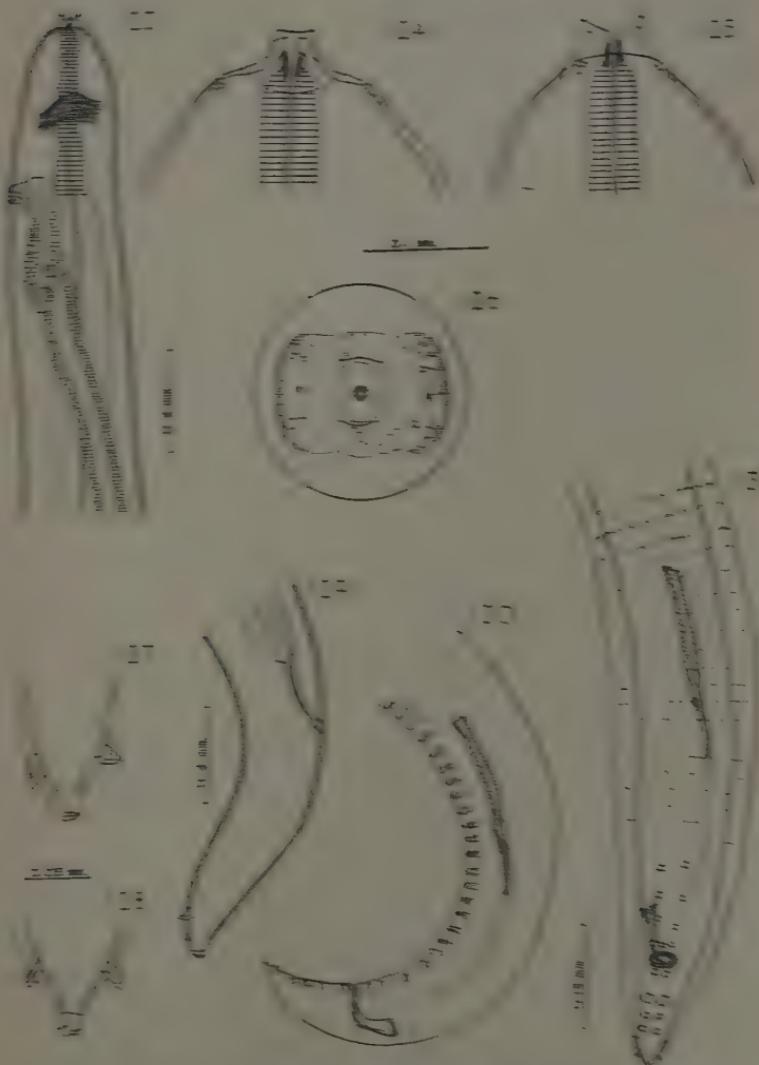
LEANNE-SHEAR. *Drosophila*, NEW.

Fig. 120.—Lateral view of female head. Fig. 121.—Ventral view of head. Fig. 122.—Ventral view of head. Fig. 123.—Female vulva. Fig. 124.—Lateral view of female tail. Fig. 125.—Lateral view of male tail. Fig. 126.—Anterior view of male tail. Fig. 127.—Ventral view of male tail.

Also a very extensive collection of well over a hundred male and female specimens from Reedbucks, *Redunca arundinum* and Red Lechwes, *Kobus leche*, Northern Rhodesia (P. L. LeRoux Coll.).

Introduction. As one type specimen has the head cut and the other the tail, the present description is based on Dr. LeRoux's specimens which I am satisfied are conspecific with the types. This species from South Africa has not been recorded in the literature since the publication of the original description. The male worm remained unknown hitherto and is described for the first time in the present communication.

Description. The worm has a rather thin smooth cuticle. The round or slightly triangular mouth opening has a small but conspicuous buccal capsule, and is surrounded by a very characteristic peribuccal crown. The very much raised peribuccal crown has a dorsal and a ventral undivided elevation which are relatively close together. There is a smooth slope from the mouth to the summit of the elevation. Looking from the dorsal or ventral aspect, the top of the elevation is almost flat or very slightly concave.

Female. The female worm has a length of 101–104 mm. and a maximum breadth of 0·7–0·8 mm. The dorsal and ventral elevations are relatively close together, 50–60 microns apart. The oesophagus has a total length of 4·7–4·9 mm., the anterior part measuring 0·4–0·46 mm. and the posterior part 4·3–4·5 mm. The nerve ring and cervical papillae are 0·24–0·29 mm. and 0·42–0·50 mm. respectively from the cephalic end. The vulval opening is 0·36–0·49 mm. from the mouth. The tail has a length of 0·44–0·59 mm. The diameter of the tail at the anus is 0·14–0·17 mm. The tail ends in a terminal spherical knob which may be slightly indented or even slightly lobed. The lateral caudal appendages are fairly large, 55–63 microns from the extremity.

Male. It is less than half the length of the female, 35–45 mm. long with a maximum diameter of 0·35–0·37 mm. The dorsal and ventral elevations are 47–50 microns apart. The oesophagus has a total length of 2·6–2·8 mm., the anterior part measuring 0·4 mm. and the posterior part 2·2–2·5 mm. The nerve ring and cervical papillae are 0·16–0·23 mm. and 0·39–0·42 mm. respectively from the cephalic end. The tail is 0·15–0·16 mm. long. The ventral precloacal surface has weakly developed transverse cuticular rugae. There is a single median precloacal papilla, and eight paired caudal papillae, four precloacal and four postcloacal. The paired caudal appendages are quite distinct, 22–27 microns from the extremity. The cuticularized cloacal opening is transversely elongated. The

stout right spicule is 0·12–0·14 mm. in length. The left spicule has a shaft of 0·15–0·19 mm. and a blade 0·1 mm.

Type host : *Redunca fulvorufa*, Mountain Reedbuck

Other hosts : *Redunca arundinum* (Reedbuck) and *Kobus leche* (Red lechwe)

Habitat : Peritoneal cavity

Type locality : Rustenberg, Transvaal, S. Africa

Other localities : Northern Rhodesia

Discussion. The material from *Redunca arundinum* and *Kobus leche* (P. L. LeRoux Coll.) are new host records for this parasite. The male is described for the first time in this paper, and it is the first record of this parasite since the original description. This species is usually found together with *Artionema bicoronata*. This species is easy to pick out from a mixed collection as the distance of the dorsal and ventral elevations is only about one-half of that in *A. bicoronata*. A closer examination will reveal an entirely different kind of peribuccal crown as shown in our drawings.

ARTIONEMA PILLERSI (Thwaite, 1927) n. comb.

(Figures 132–139)

Syns. and Litt.

Setaria pillersi Thwaite, 1927, pp. 452–4 (in *Kobus vardoni*, Northern Rhodesia).

Setaria pillersi of Baylis, 1932, pp. 498–9 (in *Adenota kob thomasi*, Toro district, Uganda).

Setaria longicauda Chabaud and Rousselot, 1956, pp. 61–70 (in *Adenota kob*, Brazzaville, imported from Archambault, Chad).

Material. Type material consisting of one male and several females (? four) from *Kobus vardoni*, N. Rhodesia (Liverpool School of Tropical Medicine Coll.).

One male and one female from *Adenota kob thomasi*, Toro district, Uganda. (Brit. Mus. Coll.)

Introduction. Thwaite had only a single male specimen, in poor condition and could not describe it well. Baylis (1932) supplemented the description of the male. The following measurements are made from one male (B.M. Coll.) and five females (one B.M. Coll. and four paratypes).

Description. The worm tapers rather markedly at both extremities making it often quite difficult to tell the head from the tail were it not for the lightly coiled tails in both sexes. The superficial cuticle is smooth, but there are fine intercuticular striations. The oval mouth opening is surrounded by a prominently protruded peribuccal crown. The dorsal and ventral peribuccal elevations are square in shape, undivided, and about 30-40 microns apart.

Female. The female has a length of 58-85 mm. and a maximum width of 0.55-0.8 mm. The oesophagus has a total length of 3.7-5.8 mm., the anterior part measuring 0.4-0.7 mm. and the posterior 3.3-5.1 mm. in length. The nerve ring and cervical papillae are 0.2-0.3 mm. and 0.36-0.44 mm. respectively from the cephalic end. The vulval opening is transversely elongated, 0.37-0.49 mm. from the anterior end. The muscular ovejector is long and slender.

The posterior extremity of the worm is slightly coiled. The tail is 0.44-0.55 mm. long and ends in a small terminal knob. There is a pair of very small caudal appendages, 20-30 microns from the caudal extremity.

Male. The male has a length of 40 mm. and a maximum breadth of 0.31 mm. The oesophagus has a total length of 3.7 mm., the anterior portion measuring 0.4 mm. and the posterior part 3.3 mm. The nerve ring and cervical papillae are 0.25 mm. and 0.52 mm. respectively from the cephalic end. The posterior extremity is slender. The ventral surface is marked by a number of cuticular rugae. The tail is 0.16 mm. long. There is a single median precloacal papilla, three paired precloacal papillae, one paired adcloacal, and four paired postcloacal papillae. There is a pair of inconspicuous caudal appendages.

The right spicule has a length of 0.13 mm. In the left spicule the shaft is 0.21 mm. long and the blade 0.09 mm.

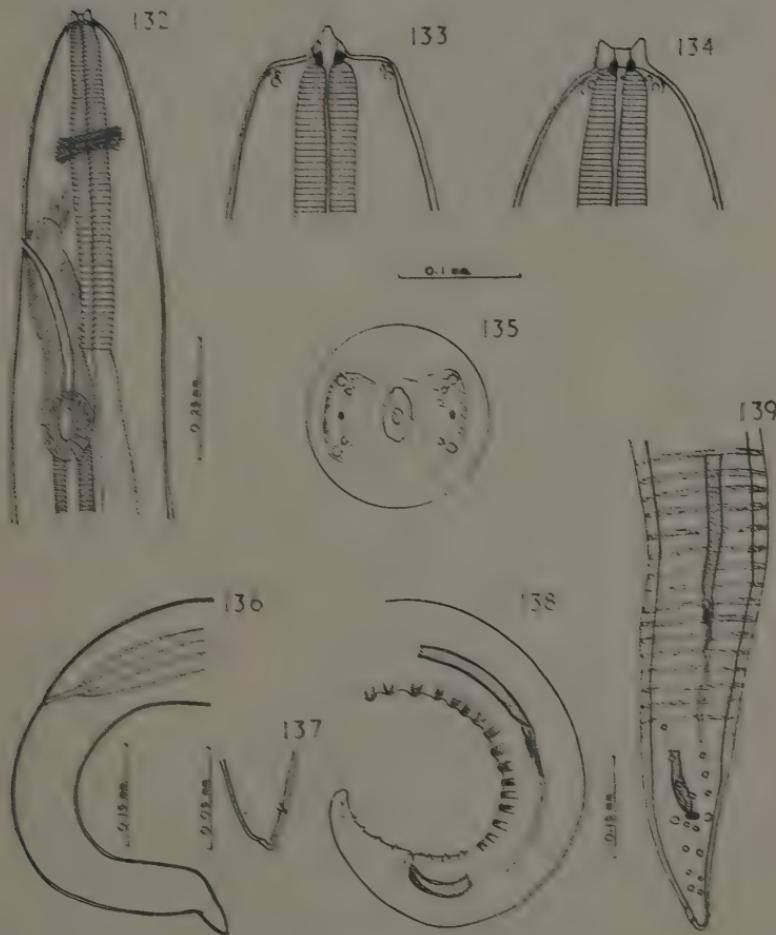
Type host : *Kobus vardoni*, Puku

Other hosts : *Adenota kob*, Kob

Habitat : Peritoneal cavity

Type locality : Nawalia, N. Rhodesia

Other localities : Uganda and Chad.



Artionema pulleri (Thwaite, 1927).

Fig. 132.—Anterior end of female worm. Fig. 133.—Ventral view of head. Fig. 134.—Lateral view of head. Fig. 135.—En face view. Fig. 136.—Female tail. Fig. 137.—Terminal part of female tail. Fig. 138.—Lateral view of male tail. Fig. 139.—Ventral view of male tail. (Figs. 132-7 are drawn from type specimens.)

Discussion: The species *Artionema pillersi* (Thwaite, 1927) was described on several female specimens and one poorly preserved male, all from the Puku, *Kobus vardoni*, Northern Rhodesia. The male was redescribed and drawn in further detail by Baylis (1932) from specimens collected from the Kob, *Adenota kob thomasi* in the Toro district, Uganda. Chabaud and Rousselot (1956) had one male and one female specimen from the same host, *Adenota kob* from "Brazzaville (animal importé d'Archambault au Tchad)." The latter authors with some hesitation believed that their material and Baylis' (1932) material may not be conspecific with that of Thwaite (1927), and provisionally proposed the name *Setaria longicauda*. Their main argument was the peribuccal elevation in *A. pillersi* is pointed in contrast to the square elevations in their specimens which also has a longer tail.

I have re-examined the type material of *Artionema pillersi* (Thwaite, 1927) and the material on which Baylis (1932) based his redescription. Some of Thwaite's material was not very good, but they showed quite clearly a square peribuccal elevation and not a pointed one as drawn by Thwaite. The length of the female tail varies a lot. In Baylis' material it was 0·48 mm. while in Thwaite's material it varied from 0·44–0·55 mm. I have no doubt that the material of Thwaite and of Baylis are conspecific and indistinguishable from the description of *Setaria longicauda*, and the latter name should fall as a synonym.

ARTIONEMA POULTONI (Thwaite, 1927) n. comb.
(Figures 140–148)

Syns. and Litt.

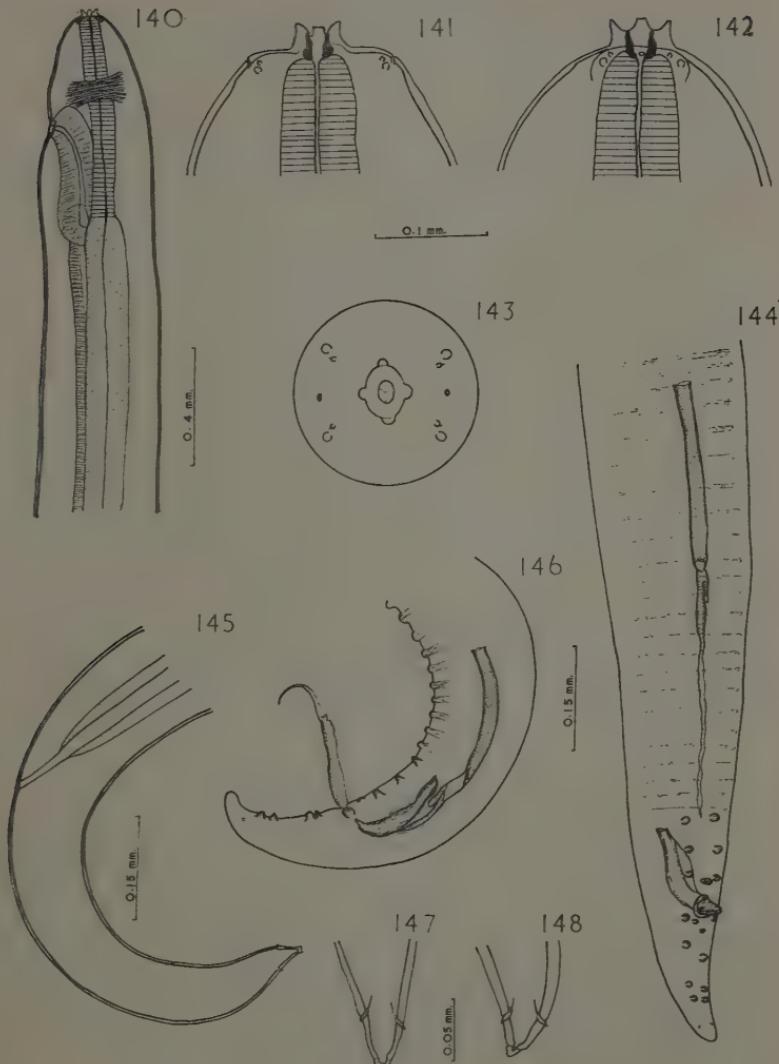
Setaria poultoni Thwaite, 1927, pp. 435–7 (in *Bubalis lelwel jacksoni* from Tonya, East shore of Lake Albert, Uganda, and *Damaliscus tiang* from Kyazanga, Masaka, Uganda).

Setaria poultoni of Strong and Shattuck, 1930, p. 453 (in *Damaliscus corrigum jimela*, Ruindi Plains, Belgian Congo).

Setaria poultoni of Sandground, 1930, p. 463 (in *Damaliscus corrigum jimela*, Ruindi Plains, Belgian Congo).

Material. Type material consisting of one female specimen from *Alcelaphus lelwel* and one male and four female specimens from *Damaliscus tiang*, Uganda (Liverpool School of Tropical Medicine Coll.).

One male and four females from *Alcelaphus lelwel*, nine females from *A. lelwel*, four females from *A. lelwel*, Uganda, and one female from *Adenota kob thomasi*, Uganda (Brit. Mus. Coll.)



Artionema pouloni (Thwaite, 1927).

Fig. 140.—Anterior part of female worm. Fig. 141.—Ventral view of head. Fig. 142.—Lateral view of head. Fig. 143.—En face view. Fig. 144.—Ventral view of male tail. Fig. 145.—Female tail. Fig. 146.—Lateral view of male tail. Figs. 147-8.—Terminal part of female tail. (Except for Fig. 144, all drawings are made from type specimens).

Introduction. Since the original description was published, only one further record of this parasite appeared in the literature (Sandground, 1930).

Description. This medium-sized worm has a smooth body cuticle. The round mouth opening is surrounded by a distinctive peribuccal crown which has two well developed peribuccal elevations and two lateral lips. The elevations and lips are separate and distinct and are situated symmetrically on the dorsal, ventral and lateral aspects. The dorsal and ventral elevations are 55–59 microns apart.

Female. The female has a length of 56–84 mm. and a maximum breadth of 0·5–0·9 mm. The oesophagus is 3·3–5·1 mm. long, the anterior part measuring 0·4–0·6 mm. and the posterior part 2·9–4·5 mm. The nerve ring and cervical papillae are 0·18–0·25 mm. and 0·34–0·42 mm. respectively from the cephalic end. The vulval opening is 0·32–0·43 mm. from the mouth. There is a muscular ovejector which joins an uncoiled vagina. The tail has a length of 0·46–0·63 mm. and its diameter at the anus is 0·1–0·13 mm. The tail usually ends in a blunt nose-cone, but sometimes it may even have a bifid papilla-like structure as shown in Thwaite's original drawing. The caudal appendages are very small, 25–38 microns from the extremity.

Male. Two male specimens were available for study. The following measurements are taken from the single type specimen. It has a length of 41 mm. and a maximum width of 0·4 mm. The oesophagus is 3·2 mm. long, the anterior part measuring 0·46 mm. and the posterior part 2·7 mm. The nerve ring and cervical papillae are 0·21 mm. and 0·29 mm. respectively from the cephalic end.

The tail is 0·19 mm. long. The ventral precloacal surface of the caudal extremity has a large number of transverse cuticular rugae. There is a single transversely elongated median precloacal papilla and eight paired papillae, three precloacal, one adcloacal and four postcloacal. The adcloacal pair may be slightly postcloacal. The first pair of postcloacal is small and more median than the others making it look almost as if they were median postcloacal papillae. The paired caudal appendages are small. The curved right spicule is about 0·17 mm. in length. The left spicule is 0·32 mm. long, the shaft being 0·21 mm. and the blade 0·11 mm.

Type host : *Damaliscus tiang*

Other hosts : *Adenota kob thomasi*, *Alcelaphus lelwe jacksoni* and *Damaliscus corrigum jimela*

Habitat : Peritoneal cavity

Type locality : Kyazanga, Masaka, Uganda

Other localities : Various parts of Uganda, and Belgian Congo

Discussion. Thwaite (1927) gave a good description and drawings of this species. It appears that he mistook the sclerotized membrane of the left spicule as belonging to the short right spicule.

As Thwaite did not select a type host, I take this opportunity to select *Damaliscus tiang* as the type host in spite his listing *Bubalis lelvel jacksoni* first each time. I have done this because he had only a single female worm from the latter host, whereas his collection from the former host consisted of both male and females. *Adenota kob* is a new host record.

This species resembles *Artionema hornbyi* and *A. pillersi* in many superficial ways, all of which are parasites of Hippotraginae. The head resembles *A. hornbyi* with the peribuccal elevations turned 45 degrees, but actually they are independently developed on different evolutionary lines. *A. hornbyi* has a primitive type of peribuccal ring with the dorsal and ventral submedian elevations unfused, whereas in *A. poultoni* the peribuccal elevations have reached a very advanced stage with the submedian elevations fused together and lateral lips developed. To *A. pillersi* it is doubtlessly very much closer. The female tails are almost identical and the male tail papillae have a similar arrangement. The peribuccal ring is practically identical, except that in *A. poultoni* there are well developed lateral elevations whereas in *A. pillersi* they are undeveloped or absent.

ARTIONEMA YORKEI (Thwaite, 1927) n. comb.

(Figures 149-154)

Syn. and Litt.

Setaria yorkei Thwaite, 1927, pp. 456-7 (in *Aepyceros melampus* and *Tragelaphus scriptus*, Nawalia, Northern Rhodesia)

Material. Type specimens consisting of one female specimen from the Impala, *Aepyceros melampus*, and three female specimens from the Bush-buck, *Tragelaphus scriptus*, from Nawalia, Northern Rhodesia. (Liverpool School Tropical Medicine Coll.)

Introduction. The name of this worm has not appeared in the literature since it was first described. The following description is

made on the type specimens, one specimen from the Impala and two from the Bush-buck as the third specimen from the latter host is incomplete.

Description. This is a rather big worm with a thick smooth cuticle. The muscular layers are rather thick and the internal structures not easily visible. The mouth opening is round and there is a distinct buccal thickening and a protruded peribuccal crown. The peribuccal crown is formed by the protruded body cuticle which forms a complete ring that ends bluntly and not upturned as in *Artionema congolensis*. There are no peribuccal elevations. The circumoral papillae and amphids are on a raised "platform" which protrudes very distinctly like padded shoulders.

Female. The female worm has a length of 136–154 mm. and a maximum width of 0·9–1·0 mm. The oesophagus is 12·6–15·0 mm. long, the anterior part measures 1·0–1·2 mm. and the posterior part 11·6–13·8 mm. The nerve ring and cervical papillae are 0·31 mm. and 0·4–0·6 mm. respectively from the cephalic end. The vulval opening is 0·5–0·6 mm. from the mouth. The tail has a length of 0·42–0·51 mm. and its diameter at the anus is 0·14–0·16 mm. The tail ends bluntly with about four small terminal digits. Laterally the caudal appendages are very small and papilla-like, 60–70 microns from the extremity.

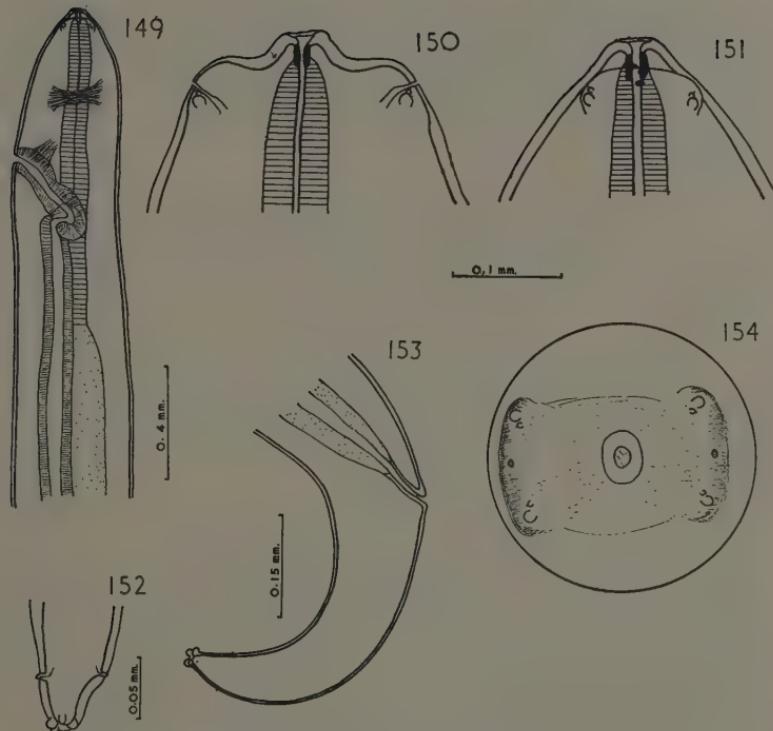
Male : Unknown

Host : *Aepyceros melampus* (Impala) and *Tragelaphus scriptus* (Bush-buck)

Habitat : Peritoneal cavity

Type locality : Nawalia, Northern Rhodesia

Discussion. This large worm has some resemblance to *Artionema congolensis*, but without a male specimen, it is difficult to make a detailed comparison. As the material of *Artionema yorkei* is so poor and insufficient for a critical study, I prefer not to choose a type host. In view of the finding of a subfamily host specificity (present paper), there is a possibility of a mistake in the collector's labelling or of one of the hosts being an accidental or occasional host and not the normal one. This can only be determined when more material becomes available. I am rather doubtful of the validity of this species, but owing to the paucity of the present material it is perhaps advisable to accept it until further collections become available. I have so far examined several collections from the Impala and Bush-buck, but have not found any of these worms, not even in Northern Rhodesia.



Artionema yorkei (Thwaite, 1927).

Fig. 149.—Anterior end of female worm. Fig. 150.—Ventral view of head. Fig. 151.—Lateral view of head. Fig. 152.—Terminal part of female tail. Fig. 153.—Female tail. Fig. 154.—*En face* view. (All figures are drawn from type specimens).

ARTIONEMA AFRICANA sp. nov.

(Figures 155-162)

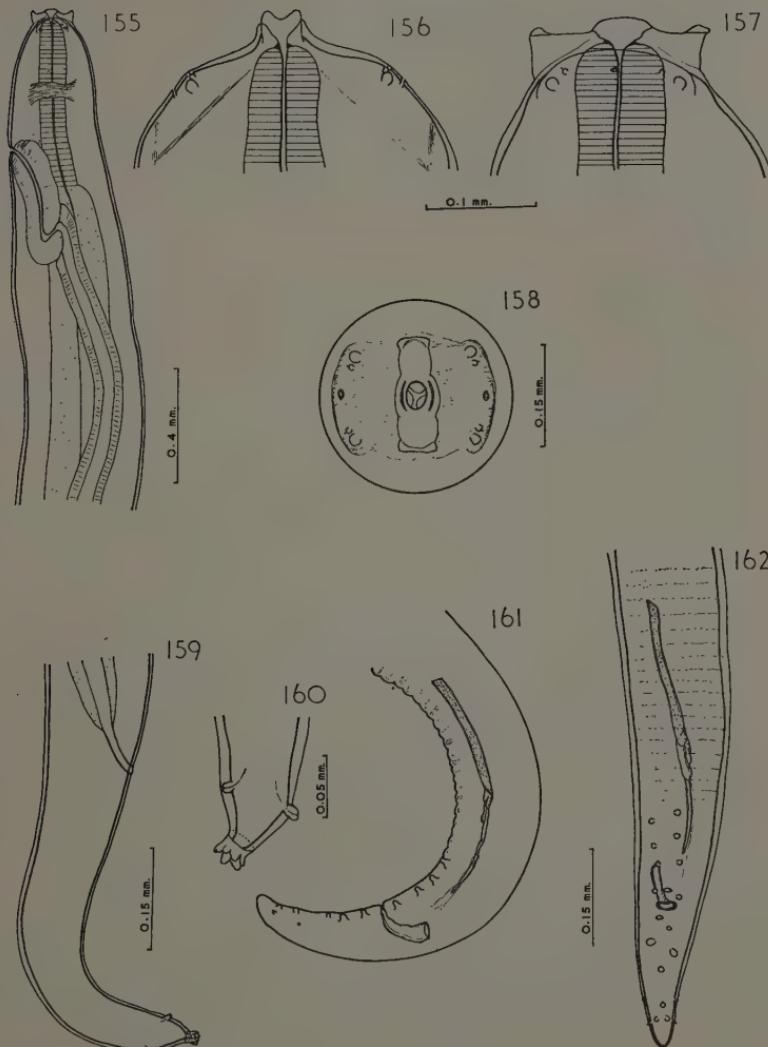
Material. Two males and eight females from *Tragelaphus* sp. Sudan, ex-Cairo Zoo (L.S.H.T.M. Coll.) ; five males and five females from *Tragelaphus angasi*, Zululand ; three females from *T. sylvaticus*, Nteko, Northern Rhodesia ; one female from Ox, Machili, Northern Rhodesia ; and twelve females (?host), Northern Rhodesia (P. L. LeRoux Coll.).

Introduction. From the literature it appears that this worm has been reported many times as *Setaria labiato-papillosa*, to which species it has a close resemblance. The new species is essentially a parasite of the Bush-buck, *Tragelaphus* spp. and may be found in cattle as well.

Description. The worm has a smooth cuticle. The round mouth opening has a small inconspicuous buccal capsule and is surrounded by a characteristic peribuccal crown. The raised peribuccal crown has a dorsal and a ventral bifid elevation, while the mouth opening has marked cuticularised lateral lips.

Female. The female has a length of 44-94 mm. and a maximum width of 0.5-0.7 mm. The dorsal and ventral elevations are far apart, 0.13-0.17 mm. The oesophagus is 5-9 mm. long, the anterior part measuring 0.4-0.7 mm. and the posterior part 4.5-8.4 mm. The nerve ring and cervical papillae are 0.2-0.3 mm. and 0.4-0.5 mm. respectively from the cephalic end. The transversely elongated vulval opening is 0.4-0.6 mm. from the mouth. The tail has a length of 0.4-0.6 mm. The diameter of the tail at the anus is 0.13-0.14 mm. The tail ends in a number of terminal spikes. The caudal appendages are 60-80 microns from the extremity and are usually blunt.

Male. The male has a length of 31-46 mm. and a maximum diameter of 0.27-0.35 mm. The dorsal and ventral elevations are 0.08-0.1 mm. apart. The oesophagus is 4-7 mm. long, the anterior part measuring 0.4-0.7 mm. and the posterior part 3.5-6.2 mm. The nerve ring and cervical papillae are 0.2-0.27 mm. and 0.32-0.65 mm. respectively from the mouth. The tail is 0.16-0.18 mm. long. The ventral precloacal surface has a number of weakly developed transverse cuticular rugae. There is a median precloacal papilla, four paired precloacal papillae and the same number of



Artionema africana sp.nov.

Fig. 155.—Anterior end of female worm. Fig. 156.—Ventral view of head. Fig. 157.—Lateral view of head. Fig. 158.—En face view. Fig. 159.—Female tail. Fig. 160.—Terminal part of female tail. Fig. 161.—Lateral view of male tail. Fig. 162.—Ventral view of male tail.

postcloacal papillae. The precloacal papillae are very regularly arranged, but the postcloacal ones are rather irregular. The first pair of postcloacal papillae are small, the second pair large, and the third pair which is large, is usually tandem in position and distantly situated. The fourth pair is relatively small and inconspicuous. The paired caudal appendages are small, 38-43 microns from the extremity. The right spicule is 0·11-0·13 mm. in length. The left spicule has a shaft 0·17-0·19 mm. in length and a blade 0·08-0·11 mm.

Type host : *Tragelaphus angasi*, Nyala

Other hosts : *Tragelaphus sylvaticus* and cattle

Habitat : Peritoneal cavity

Type locality : Zululand, Southern Africa

Other localities : Northern Rhodesia, and Sudan (ex-Cairo Zoo)

Type specimens : Deposited in the Helminthological Collection of the London School of Hygiene and Tropical Medicine

Affinities. This parasite resembles *A. labiato-papillosa* very closely but differs in several important respects. First, *A. labiato-papillosa* has a very elongated mouth opening with equally elongated lateral lips which bend towards the centre. In *A. africana* sp. nov. the mouth opening is round and the lateral lips are short and conspicuous because it is slightly upturned outwards, unlike *A. labiato-papillosa*. In the female of *A. labiato-papillosa* the caudal appendages are large and pointed, about 0·1-0·13 mm. from the extremity, while in *A. africana* they are smaller and blunt in shape and only slightly more than half of this distance from the extremity. In the male the caudal appendages are inconspicuous when compared with the relatively large appendages of *A. labiato-papillosa*. Also in the latter species the first pair of precloacal papillae are very close to the cloaca while in the new species they are definitely precloacal. With these points in mind, there should not be much difficulty in separating these two closely related species when found in cattle. To this new species the name *A. africana* is given after its place of origin.

ARTIONEMA DIGITATA (von Linstow, 1906) n. comb.
 (Figures 163–170)

Syns. and Litt.

Filaria digitata von Linstow, 1906, pp. 171–2 (in *Bos indicus*, Colombo, Ceylon)

Setaria digitata (von Linstow, 1906) Railliet and Henry, 1911
 (above species moved to the genus *Setaria*)

Setaria marshalli Boulenger, 1921, p. 346 (in cattle, Wassein, Burma)

?*Setaria buxi* Bhalerao, 1933, pp. 163–4 (in Hill goat, Muktesar, India)

Material. Many collections totalling over a hundred specimens with many males from cattle in Malaya and India (L.S.H.T.M. Coll.), Ceylon (kindly sent by Dr. A. S. Dissanaike), Burma and Mauritius (P. L. LeRoux Coll.), and one female specimen from Jamnapari goat, Ceylon (P. L. LeRoux Coll.).

Six collections of juvenile worms in eyes of ox and horses in India as follows : one male and one female worm in eyes of an ox ; two males, one female, one female, two males, and one female, and three males and two females respectively in eyes of five horses. (L.S.H.T.M. Coll.).

Introduction. I have not attempted to list the complete literature under the heading for two reasons. First a large number of identifications are questionable, and secondly the list is very extensive and quite unnecessary for the present purpose. This species appears to have a strictly Asian distribution and is often found in association with *A. labiato-papillosa* as a mixed infection in cattle.

A. digitata as a parasite of the eye. I have examined six collections from eyes of an ox and horses in India, and in each case they were found to be juvenile worms indistinguishable from *Artionema digitata*.

Description. The following description is for the adult worm in the peritoneal cavity. This worm has a rather thick smooth cuticle. The round mouth opening has an inconspicuous buccal capsule and is surrounded by a characteristic peribuccal crown. The raised peribuccal crown when viewed laterally shows a small central "helmet" or cuticularized lateral lips. The dorsal and ventral elevations are slightly bifid.

Female. The female has a length of 65–75 mm. and a maximum breadth of 0·5–0·7 mm. The dorsal and ventral elevations are 70–80 microns apart. The oesophagus is 6–7 mm. long, the anterior part measuring 0·5–0·6 mm. and the posterior part 5·5–6·5 mm.

The nerve ring and cervical papillae are 0·2–0·3 mm. and 0·4–0·5 mm. respectively from the cephalic end. The vulval opening is 0·5–0·6 mm. from the mouth. The tail has a length of 0·4–0·5 mm. and its diameter at the anus is 0·13–0·15 mm. The tail ends in a terminal spherical knob which may be perfectly smooth or slightly roughened with a papillated surface. The lateral caudal appendages are well developed, 60–70 microns from the extremity.

Male. The male has a length of 35–46 mm. and a maximum breadth of 0·3–0·5 mm. The dorsal and ventral elevations are 60–65 microns apart. The oesophagus is 5–7 mm. long, the anterior part measuring 0·5–0·6 mm. and the posterior part 4·5–6·5 mm. The nerve ring and cervical papillae are 0·2–0·3 mm. and 0·4–0·5 mm. respectively from the cephalic end. The tail is 0·17–0·21 mm. long. The ventral precloacal surface has a number of transverse cuticular rugae. There is a single median precloacal papilla, and eight paired papillae of which four are precloacal and four postcloacal. The first paired precloacal papillae are more often adcloacal in position than precloacal. The well developed caudal appendages are 50–70 microns from the extremity. The cloacal opening is transversely elongated. The stout right spicule is 0·13–0·14 mm. in length. Its proximal quarter is narrow. The left spicule has a shaft of 0·25–0·27 mm. and a blade 0·13–0·15 mm.

Type host : *Bos indicus*

Other hosts : Mainly in cattle; records of its occurrence in other hosts need expert confirmation

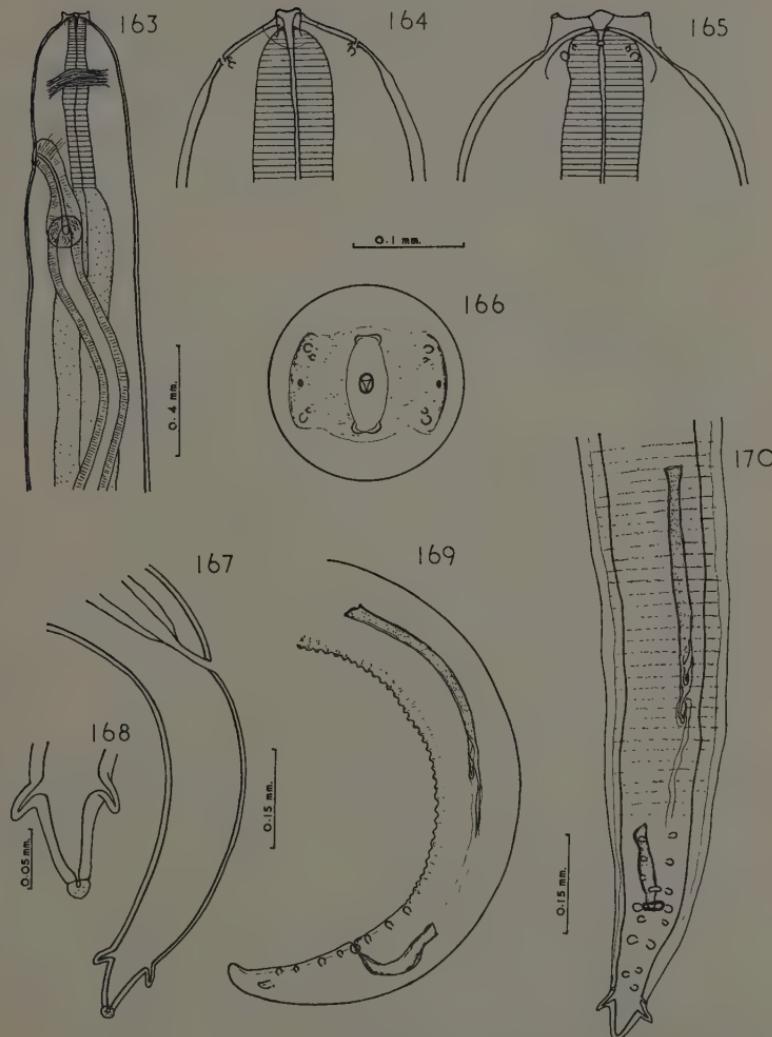
Habitat : Adults mainly in peritoneal cavity; juveniles are found often in eyes of cattle and horses

Type locality : Colombo, Ceylon

Other localities : Throughout Asia, and in Mauritius

Discussion. This species appears to have a strictly Asian distribution. It is also found in Mauritius, probably imported from Asia as their domestic animal fauna is very Asian (LeRoux and Darne, 1955).

The species was first described by von Linstow (1906) as *Filaria digitata* from *Bos indicus* in Colombo, Ceylon. He says "tail rounded, carrying in the female a spherical appendix". His text-fig. 55 shows this very well, and I consider it as one of the important distinctive characters. A few years later, Railliet and Henry (1911a) moved the species to the genus *Setaria*.



Artionema digitata (von Linstow, 1906).

Fig. 163.—Anterior end of female worm. Fig. 164.—Ventral view of head. Fig. 165.—Lateral view of head. Fig. 166.—En face view. Fig. 167.—Female tail. Fig. 168.—Terminal part of female tail. Fig. 169.—Lateral view of male tail. Fig. 170.—Ventral view of male tail.

Boulenger (1921) made a good redescription of the female of *A. digitata*. He says *A. labiato-papillosa* has a prominent peribuccal crown "much elongated dorso-ventrally and deeply notched laterally in such a way as to give the appearance in a side view (Text-fig. 1A) of strong dorsal and ventral teeth separated by a wide depression from the centre of which arises a semi-circular lip-like elevation. Each tooth is in its turn indented so as to form two cusps, visible when the head is viewed from the dorsal or ventral surface (Text-fig. 1B), they are usually better developed in the females than in the males." For *A. digitata* he says the peribuccal crown resembles that of *A. labiato-papillosa* and "the lateral notches are however less deep and the lip-like chitinous projections from their centres are better developed and frequently almost triangular in shape (Text-fig. 3A), in which case they have the appearance of lateral teeth. The dorsal and ventral teeth are notched so as to present two cusps (Text-fig. 3B)". The above paragraph by Boulenger, although not entirely satisfactory, is nevertheless reasonably reliable and the best account available in the literature of the peribuccal crown of the two species in question. His above statements have been unreasonably criticised several times in the literature.

Soon afterwards confusion began. Purvis (1931) in a most unconvincing study concluded that "as a result of working over Malayan material from the water buffalo and ox, I conclude that *Setaria digitata*, von Linstow, 1906, is a synonym of *Setaria labiato-papillosa* (Alessandrini, 1838)".

The situation was not improved by Baylis (1936b) whose conclusions were based on very few specimens; his publication was almost entirely a review of the literature with a list of synonyms taken mainly from old text-books. It appears that the only type specimen he examined was *A. digitata* (von Linstow) from Ceylon. After quoting Purvis (1931) he says "the tails of seven females were examined, and, while none of them had large spines, the terminal knob could in no case be described as perfectly smooth, but always showed some traces of wrinkling or "shagreening". . . . Accordingly, the writer has no hesitation in endorsing the view of Purvis that *S. digitata* is a synonym 'S. labiato-papillosa'." *S. marshalli* he suspects as a synonym of *S. labiato-papillosa*, but prefers the question to remain open. *Setaria nudicauda* Ortlepp, 1924 he questions as a synonym of *S. labiato-papillosa*; while as for *Setaria altaica* Raevskaya, 1928, *Setaria cervi* Maplestone, 1931 and *Setaria buxi* he has no hesitation in considering them as synonyms of *S. labiato-papillosa*. He gave a formidable list of synonyms prefaced by the

following words :

"To sum up what has been said, it is suggested that the name *Setaria cervi* should replace *Setaria labiato-papillosa*, and the following provisional, and probably incomplete, synonymy may be given :—

SETARIA CERVI (Rud., 1819)

Synonyms :—

- Filaria papillosa* auctt. (part).
- Filaria oculi* auctt. (part).
- Filaria cervi* Rudolphi, 1819. *Entozoorum Synopsis*, p. 8.
- Filaria cervina* Dujardin, 1845. *Hist. Nat. des Helminthes*, p. 49.
- Filaria terebra* Diesing, 1851 (part). *Syst. Helm.*, **2**, 274.
- Filaria bidentata* Molin, 1858. *Sitz. K. Akad. Wiss. Wien*, **28**, 401.
- Filaria terebra* Dies., of Molin, 1858. *Ibid.*, 405.
- Filaria cervi elaphi* Molin, 1858. *Ibid.*
- Filaria labiato papillare* Perroncito, 1882. *I Parassiti dell' Uomo e degli Animali utili*, p. 326.
- Filaria labiato papillosa* Perroncito, 1882. *Ibid.*
- Filaria labiato-papillosa* Railliet, 1888. *Bull. Soc. centr. Méd. vét.*, **42** (n.s., **6**), 98.
- Filaria digitata* v. Linstow, 1906. *Spolia Zeylan.*, **3**, 171.
- Setaria labiato-papillosa* Railliet and Henry, 1911. *Bull. Soc. Path. exot.*, **4**, 387.
- Setaria bidentata* Railliet and Henry, 1911. *Ibid.*
- Setaria digitata* Railliet and Henry, 1911. *Ibid.*
- Setaria altaica* Rajewsky, 1928. *Trud. Gos. Inst. Exp. Vet.*, **5**, 24.
- Setaria cervi* [n.sp.] Maplestone, 1931. *Rec. Ind. Mus.*, **33**, 92.
- Setaria buxi* Bhalerao, 1933. *Ind. Jl. Vet. Sci.*, **3**, 163.
- ?*Filaria bujali* Rudolphi, 1819. *Entozoorum Synopsis*, p. 8.
- ?*Filaria tentaculata* Mehlis, *apud* Creplin, in Ersch & Gruber, 1846. *Allg. Enzycl. d. Wiss. u. Künste*, Leipzig, Sect. I, TL **44**, p. 172.
- ?*Filaria bujai (abdominalis)* Molin, 1858. *Sitz. K. Akad. Wiss. Wien*, **28**, 421.
- ?*Setaria nudicauda* Ortlepp, 1924. *Jl. Helminthol.*, **2**, 21.

Since Baylis' paper (1936b), most original research workers and textbook writers accepted his list of synonyms, but before long a number of papers appeared which cast doubt on some of them. Sarwar (1946) in an unconvincing piece of work was of the opinion that *S. digitata* (von Linstow, 1906) and *S. cervi* (Rud., 1819) were distinct species. His drawings were very sketchy and his reasons for distinguishing the two species rather unreliable. (See discussion under *A. altaica* for reference to *S. cervi*. Since Baylis (1936b) up to the present, *S. cervi* of various authors including Yeh (1958a) has been used incorrectly as synonymous with *A. labiato-papillosa*). From the large numbers of papers which touched on the subject in passing, it is clear that writers were divided in opinion. Up to date there is still no convincing proof in the literature to show that *A. digitata* and *A. labiato-papillosa* can be separated on good morphological grounds.

In my examination of the genus *Setaria* s.l. very extensive collections of *A. digitata* and *A. labiato-papillosa* from various parts of the world has been available. At no time did I experience any difficulty in separating the two species. Important differential characters are as follows :—

1. The distance of the dorsal and ventral elevations averages about 60 microns in the male and 75 microns in the female for *A. digitata*. In *A. labiato-papillosa* they are anything from 50–100% further apart.
2. In *A. digitata* the mouth opening is round, while in *A. labiato-papillosa* it is markedly elongated. This can be seen either *en face* or from the lateral view. On the lateral view it can be seen by focusing on the mouth opening itself, or it can be seen by focusing on the peribuccal crown for the "helmet" or the cuticularised lateral lips. The helmet is actually the protruding rim of the mouth opening, and it is therefore small in *A. digitata*, and elongated in *A. labiato-papillosa*. This point was first correctly noticed by Boulenger (1921), although he made no mention of the foremost important character, that is, the elongated mouth opening.
3. The terminal knob on the female tail is also a useful differential character, a fact which was noted by von Linstow (1906). If reasonable care is taken to note broken terminal tail-knobs, this is a very convenient character to use.
4. The distance of the caudal appendage from the extremity is 50–70 microns in both sexes of *A. digitata*. In *A. labiato-papillosa* it is twice that distance.

Apart from the terminal knob character (von Linstow, 1906) and the shape of the peribuccal crown in lateral view (Boulenger, 1921) no other reliable characters for separating the two species appeared in the literature. The characters listed above are new characters which I believe to be useful and most reliable in separating the two species commonly found in Asian ruminants. With very little practice, one can tell the two species apart in a few seconds by either looking at the head end or tail end of either sex.

Setaria marshalli Boulenger, 1921 appears to be a synonym of *A. digitata*. Often the lateral lips of the mouth become deformed and take various shapes. I have seen several specimens which resemble *S. marshalli* as drawn by Boulenger. It is almost certain that they are conspecific with *A. digitata*.

Setaria buxi Bhalerao, 1933 was described on a single female specimen. It appears to be an ill-formed specimen of *A. digitata*. I have found that the lateral lips of *A. digitata* are very thin and take various shapes in an abnormal host, e.g. in worms from the eyes of horses; often such distortion has been observed even in worms from the normal host and habitat. In a large collection of *A. digitata*, there are always one or two peculiar looking specimens.

ARTIONEMA LABIATO-PAPILLOSA (Perroncito, 1882) n. comb.

(Figures 171-179)

Syns. and Litt.

Filaria labiato papillare of Perroncito, 1882, pp. 326-8 (in *Bos taurus*).

Setaria labiato-papillosa of Railliet and Henry, 1911, p. 387.

Setaria cervi of Baylis, 1936b, pp. 293-8 (part).

Setaria cervi auct. 1936 onwards.

Setaria leichungwingi Chen, 1937, pp. 157-60 (in Buffalo, Canton, China).

?*Setaria bovis* Klenin, 1940 (in *Bos taurus*, U.S.S.R.)

Material. Available material consisted of a very extensive collection of several hundred worms from cattle with ample male and female specimens from South China (personal coll.), Malaya, India and various parts of Africa, (L.S.H.T.M. Coll.), Ceylon (kindly sent by Dr. A. S. Dissanaike), Northern Rhodesia (P. L. LeRoux Coll.), and Rome Zoo (E. Biocca Coll.).

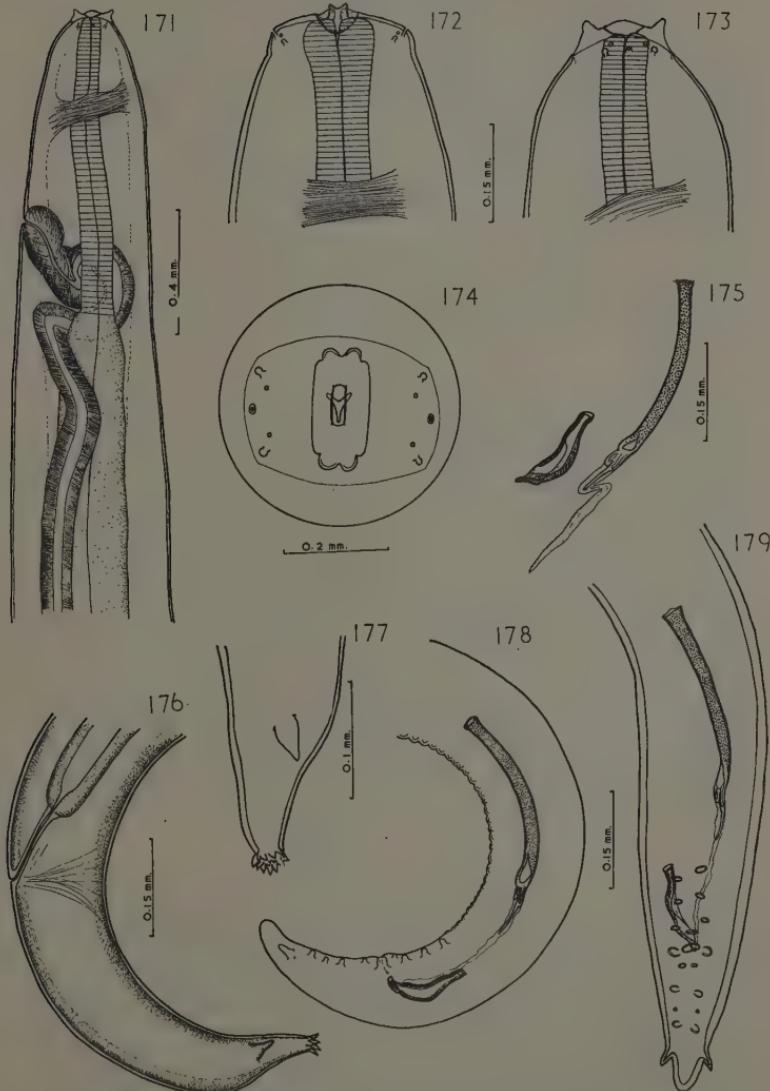
Introduction. Since this worm was moved to *Setaria* as *Setaria labiato-papillosa* by Railliet and Henry, 1911a, it enjoyed stability until Baylis (1936b) listed it as a synonym of *S. cervi*. (See "Discussion" on *A. digitata*). I have not the slightest doubt as to the validity of this species.

Description. These worms taper slightly at both extremities. The cuticle is smooth. The mouth has a small buccal thickening and the opening is dorso-ventrally elongated. The peribuccal crown has two bifid peribuccal elevations with the tip of each tooth bent outwards. When viewed laterally the peribuccal crown has a smooth crescentic outline due to the cuticularised lateral lips which project slightly over the mouth opening. The peribuccal crown and papillae are placed on a laterally elongated raised platform. When viewed ventrally or dorsally it gives the worm a square truncated look. When viewed laterally the sides attenuate smoothly, and when focusing for the mouth, one is first confronted with the lateral shoulders jutting out. The posterior part of the oesophagus has the same diameter as the intestine. In a lateral view the anterior tip of the oesophagus is usually straight, but in a ventral or dorsal view, it is often slightly swollen.

Female. The female measures 60–94 mm. in length and 0·6–0·9 mm. in width. The oesophagus is 8·0–11·0 mm. long, the anterior part measuring 0·6–0·85 mm. and the posterior part 7·3–10·4 mm. The nerve ring and cervical papillae are 0·25–0·29 mm. and 0·46–0·63 mm. respectively from the cephalic end. The vulva opens 0·45–0·80 mm. from the anterior end. The vagina (6–9 mm. long) may run straight back immediately, or it may go slightly forward before proceeding posteriad. The uteri are packed with sheathed microfilariae but they are seldom found in the vagina.

The posterior extremity of the worm is slightly coiled. The tail has a length of 0·44–0·60 mm. and terminates in a varying number of spikes, usually with most of the large spikes forming an outer circle and a few smaller ones an inner circle. There are two large caudal appendages 0·09–0·13 mm. from the extremity.

Male. The male has a length of 40–51 mm. and a breadth of 0·38–0·45 mm. The oesophagus is 7·5–10·1 mm. long, the anterior part measuring 0·6–0·8 mm. and the posterior part 7·0–9·5 mm. The nerve ring and cervical papillae are 0·25–0·28 mm. and 0·50–0·53 mm. respectively from the cephalic end. The slender tail is 0·17–0·20 mm. long. There is a large transversely elongated median precloacal papilla, and eight paired caudal papillae, three precloacal, one adcloacal and four postcloacal.



Artionema labiato-papillosa (Perroncito, 1882).

Fig. 171.—Anterior end of female worm. Fig. 172.—Ventral view of head. Fig. 173.—Lateral view of head. Fig. 174.—En face view. Fig. 175.—Dissected spicules. Fig. 176.—Lateral view of female tail. Fig. 177.—Terminal part of female tail in lateral view. Fig. 178.—Lateral view of male tail. Fig. 179.—Ventral view of male tail.

The right spicule measures 0·12–0·16 mm. in length with the distal end bent over to form a groove. The left spicule consists of a pitted shaft 0·25–0·28 mm. long, followed by a twist and a tapering blade 0·12–0·14 mm. The blade is covered by a long sclerotized membrane which protudes 0·20–0·22 mm. beyond the end of the blade. This membrane is usually overlooked and has only been described a few times in recent literature.

- Host* : Cattle and buffaloes. Also a number of occasional or doubtful records from goat and sheep.
- Habitat* : Mainly peritoneal cavity. Several records from small intestine and eyes.
- Locality* : Practically cosmopolitan.

Discussion. (See also discussion under *A. altaica*, *A. africana* and *A. digitata*). Chen (1937) described a new species, *Setaria leichungwingi* from Buffalo in Canton, mainly on the fact that his specimens had a longer left spicule than those listed in the literature. This discrepancy is due to the fact that previous authors gave the measurement of only the heavily sclerotized parts, while Chen gave a measurement which included the sclerotized membrane. Chabaud and Rousselot (1956) rightly places the species as a synonym.

Klenin (1940) described *Setaria bovis* from cattle, *Bos taurus* in the Soviet Union. The male is undescribed. The writer could not consult the original paper but from the description without figures as given by Skryabin and Shikhobalova (1948) it appears not unlike *A. labiato-papillosa*.

Setariinae, incertae sedis

Filaria effilata von Linstow, 1897, in the Zoological Museum of Kaliningrad, U.S.S.R.

Setaria thomasi Sandosham, 1954, in the Department of Parasitology, University of Malaya, Singapore.

I was unable to examine the type specimens of the above two species which are very poorly described and unrecognisable by modern standards, and remain *incertae sedis* to science.

LIFE CYCLE

Although larval development was expected to take place in some blood sucking arthropod, little was known about the life-cycle in this group until comparatively recently. Earlier, Noë (1903) believed *Stomoxys calcitrans* to be the vector for *A. labiatopapillosa* in Italy. A number of "original publications" by various authors suspected *Stomoxys* in other parts of the world, and this unconfirmed information appeared in a number of general veterinary textbooks. There is no experimental evidence that *Stomoxys* is the vector, and Noë's observations need confirmation which has not been forthcoming, e.g. Williams, 1955. It appears very unlikely that *Stomoxys* is the vector.

Recently several workers in different places have shown experimentally that mosquitoes can act as vectors. Ochi (1953) described work done in Korea (1938-43) on lumbar paralysis and found *Anopheles sinensis hyrcanus* and *Armigeres obturbans* as vectors of *A. digitata*. Kadenatsii (1956) found *Culex pipiens* and *Aedes* sp. to be suitable experimental vectors for *Setaria marshalli*. (It should be noted that both workers mentioned *Setaria marshalli* in their papers. In the present paper *Setaria marshalli* Boulenger, 1921 has been taken to be a synonym of *A. digitata*. They were probably working with *A. digitata*, or with a poorly known or some undescribed species.) More recently Heisch, Nelson and Furlong (1959) have shown that *Setaria equina* develops in *Aedes aegypti*, *Aedes pombaensis* and *Culex pipiens fatigans*.

Refuerzo (1954) has reported a case of prenatal infection of a calf with *Artionema labiatopapillosa*.

PATHOLOGY

Recently a flood of reiterative papers has appeared on cerebro-spinal nematodiasis, supposedly caused by *Setaria* spp. Many other nematodes however are known to invade the nerve centres. Neuman (1892) writes: "Albrecht [1872] reports the case of a Horse which, during work, suddenly began to stagger; the eyes were fixed, and the respiration was noisy; there were remissions and relapses. Three hours after the first symptoms appeared, the head was carried low and inclined to the left, and there were convulsive movements of the neck and limbs. Soon it fell on the left side, became unconscious, and manifested complete insensibility. In this state it was killed, and at the autopsy there were found

diffuse meningitis, haemorrhagic encephalitis, and in the middle lobe of the cerebellum a Sclerostome, which had probably arrived there when an embryo. Van Heill [1874] saw a three year old Horse which was suddenly attacked with furious vertigo, that lasted about a quarter of an hour. An autopsy revealed congestion of the brain and choroid plexus, while a free Sclerostome was lodged in the cortical substance of the right hemisphere. Le Bihan found another worm of this kind in the occipital artery; rupture of the aneurism caused the death of the Horse in less than ten minutes.

Abildgaard discovered the *Filaria equina* between the dura-mater and cranial arachnoid of a Horse (Rudolph).

Sprent (1955) has given an excellent account of various groups of nematodes which invade the central nervous system.

Innes, Shoho and other co-workers (see 1952, 1953 for general review) have summarized the work done by the Japanese workers in Korea during the war. They found *Artionema digitata* to be the causal agent of "epizootic cerebro-spinal nematodiasis or setariasis". Their discussion of the worm and helminthological literature is vague, and their synonymy of the worm incorrect. Their pathological findings have since been confirmed by other workers elsewhere, e.g. Kadenatsii (1956). Bush (1951) has shown however that "lumbar paralysis" can also be produced by malnutrition. Innes and Shoho (1953), Bieling (1952), McFadzean (1955) and others call the attention of the medical profession to *Setaria s.l.* which may possibly invade the central nervous system of man. As a number of different worms have been recovered from the central nervous system of various animals, one wonders why *Setaria s.l.* should be singled out as a suspect for nervous symptoms of obscure aetiology.

HOST SPECIFICITY, PHYLOGENY AND SPECIATION

In the present study the writer was fortunate to be able to examine several hundred collections of *Setaria s.l.*. The work done was mainly a morphological study, from which it became clear that there is a strict host-parasite relationship in the group. As most of the species are parasites of Artiodactyls, their distribution in this group of ungulates was of particular interest.

In Hyracoidea, only one species is known, *Hyraconema loveridgei* in *Proavia* and *Dendrohyrax*.

In Perissodactyls, only one species is known, *Setaria equina* in *Equus*.

In Artiodactyls, the parasites are restricted to family or subfamily groupings, as follows :

Tragulidae. Only one species is known in this family, i.e. *Actionema javensis* in *Tragulus*.

Suidae. Only *A. congolensis* and *A. bernardi* are properly known.

Cervidae. Contains *A. altaica*, *A. tundra* and *A. hartwichi* sp. nov.

Bovidae. There are twelve species of *Actionema* in this host-group and each species is restricted to one subfamily. Ample material was available for all of them, and in some species a very extensive collection was available from a large number of hosts and scattered over a wide geographical region.

In the subfamily Bovinae, there is *A. africana* n. sp. found in *Tragelaphus* and the ox. *A. labiato-papillosa* and *A. digitata* are found in cattle and buffaloes.

In the subfamily Hippotraginae, *A. pouloni* is found in *Kobus*, *Alcelaphus* and *Damaliscus*. *A. bicoronata* is found in *Kobus* and *Redunca*. *A. hornbyi* is found in *Hippotragus* and *Redunca*.

In the subfamily Cephalophinae, *A. caelum*, *A. dipetalonematoides* and *A. southwelli* are found in *Cephalophus*.

In the subfamily Antilopinae, *A. scalprum* is found in *Raphicerus*, *Ourebia*, *Aepyceros* and *Gazella*.

From the above host distribution list, it is clear that each species is restricted to a particular group of animals. Let us consider the Bovidae in further detail.

In Antilopinae only one species *A. scalprum* is known and it is found in various genera. The parasite is a comparatively primitive looking species. The peribuccal elevations are close together, the female caudal appendages are very small, and the four pairs of precloacal papillae are strictly anterior.

In Cephalophinae there are three very interesting species. In *A. caelum* there is a primitive bifid peribuccal elevation, in *A. dipetalonematooides* it is level and almost square, while in *A. southwelli* it is worn down to become pointed.

The parasites in Hippotraginae have several stems of origin. *A. hornbyi* is a more primitive type where the peribuccal elevations are still widely spaced on each of the four corners, and the four pairs of precloacal papillae are strictly precloacal in position. In *A. bicoronata* the elevations have fused to become a dorsal and a ventral bifid elevation and the basic precloacal papillae arrangement unchanged. In *A. pillersi* the elevations have worn down to become almost pointed, and the first paired precloacal papillae have moved to an adcloacal position. In *A. poultoni* the elevations have reached a very advanced stage of development. Not only have the dorsal and the ventral set of elevations fused together and become smooth, but on each side a lateral lip has developed. The first paired precloacal papillae have also taken a more advanced stage by moving posteriorly to an adcloacal position. In this subfamily of hosts, we therefore find a complete range of morphological structures, from the comparatively primitive looking *A. hornbyi* to the very advanced *A. poultoni*. The latter species resembles the bovine worms in many respects but differs markedly from them in other ways.

In the subfamily Bovinae, all three species have the same fundamental pattern. The dorsal and ventral elevations are bifid and the lateral lips are broad. *A. labiato-papillosa* differs from all the others in having not a round mouth opening but a dorso-ventrally elongated one. The first paired precloacal papillae of *A. africana* are still precloacal, while in *A. digitata* and *A. labiato-papillosa* they have moved to the adcloacal position.

From the brief review above, it is clear that the rate of evolution of the parasite is very slow indeed, and that by the time the parasite has developed to the status of a new species, the host population has advanced well past generic status and far on to a subfamily. Cameron (1929) observed a similar phenomenon during his studies on *Enterobius* when he discovered that each genus of host had its own species of *Enterobius*. The different rates of evolution are comprehensible when we consider the vast effects of the external environment on the host, while the parasite is in a relatively stable environment inside its host. When comparing the respective habitats of *Enterobius* and *Setaria s.l.*, the latter as a tissue parasite is in a far more stable environment.

THE EVOLUTION OF TAXONOMIC CHARACTERS IN THE GENUS
SETARIA S.L.

Many of the taxonomic structures mentioned below, are structures which have evolved independently several times.

The peribuccal crown. *A. javensis* shows a primitive structure. The peribuccal crown is simple, of a primitive type, and formed by a slight upturning of the anterior body cuticle. In *Hyraconema loveridgei* the peribuccal crown begins to spread out. The anterior body cuticle pushes out to form a primitive peribuccal crown, and

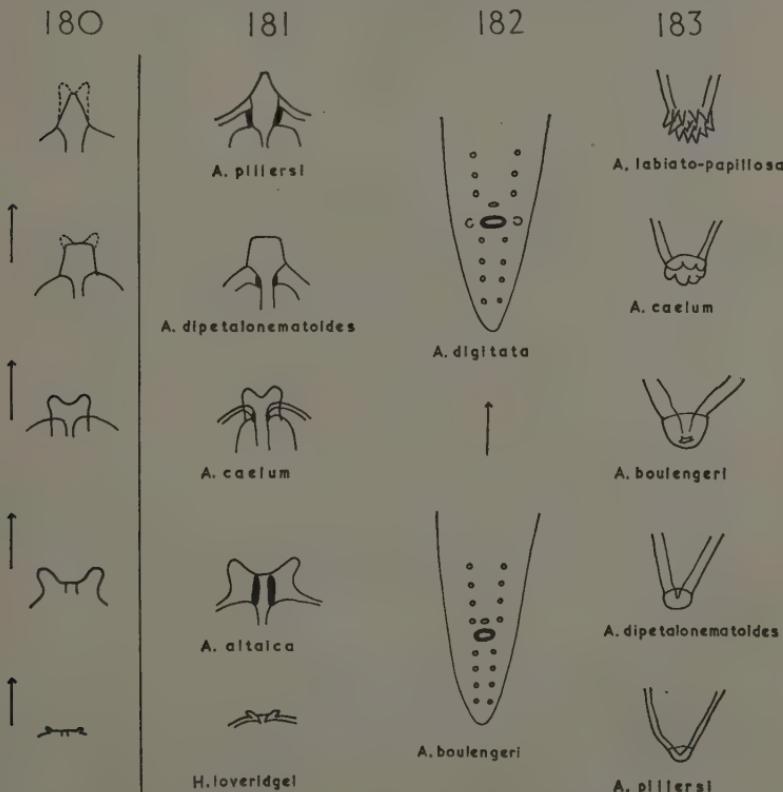


Fig. 180.—The probable evolution of the peribuccal elevation. Fig. 181.—The ventral view of the peribuccal elevation in five species. Fig. 182.—The male tail in ventral view. Fig. 183.—The female tail extremities of five species.

four elevations develop from the crown. In *A. hornbyi* the four cornered upturnings have developed to four separate well-formed elevations on each corner. In *A. bicoronata*, the paired dorsal submedian elevations and the paired ventral submedian elevations have fused to give a bifid appearance. In *A. boulengeri*, the bifid tooth elevations have become smooth and chisel-shaped. In *A. pillersi* the edges of the "chisel" have worn down almost to a point. In *A. poultoni* lateral elevations developed. Fig. 181 shows this gradual change from *loveridgei* through *altaica* to *pillersi*.

The male tail papillae. In *A. boulengeri* there is the basic primitive pattern of four pairs of precloacal papillae and four postcloacals. In *A. pillersi* and *A. poultoni* the first paired precloacal papillae have migrated to the adcloacal position, and this is also true for *A. digitata* and *A. labiato-papillosa*.

The caudal appendages in the female. The caudal appendages progress from small to large. In *A. pillersi* and *A. poultoni* they are extremely small. In *A. africana* they are bigger, and in *A. digitata* and *A. labiato-papillosa* they are large.

The caudal extremity of the female. This changes from a small inconspicuous knob, to a large knob, and finally to spines. In *A. pillersi* the terminal knob is very small, in *A. bicoronata* it is a large knob, and often slightly indented, in *A. caelum* it has many lobes, in *A. africana* a number of spines which are usually neatly arranged, and in *A. labiato-papillosa* it is usually a disorderly conglomeration of spines.

THE SYSTEMATICS OF THE GENUS *SETARIA* S.L.

The genus *Setaria* s.l. is a heterogeneous group which undoubtedly should be divided into a number of genera. In the systematics of the genera, I have endeavoured to trace the phylogeny of the group and find the characters with the slowest rate of evolution for this separation.

We have found that the genotype *Setaria equina* has a spicular shape of its own; both the male tail and the female tail are invested with cuticular bosses, and the head is armed with four spikes. The entire worm is so grossly different from all the others in so many important details apparently restricted to this perissodactyl worm only, that I believe it was an early off-shoot and evolved in parallel with its host. I therefore propose that *Setaria equina* alone should be kept in this genus, a monotypic genotype with no other known species.

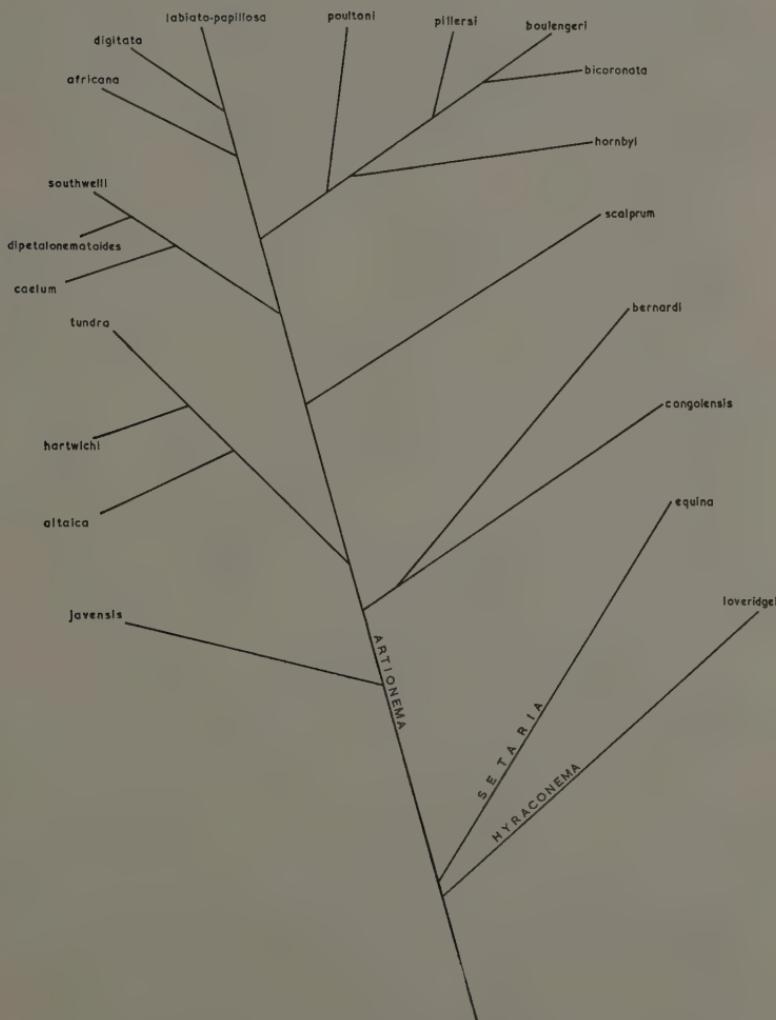


Fig. 184.—The probable phylogeny of the genera and species.

Next comes the parasite from the hyrax which differs from all the others in the shape of the long spicule which ends in a slender fully-sclerotized distal portion. The peribuccal ring is of a very primitive type with the peribuccal elevations poorly developed. The parasite is very long and is found only in the hyracoids, and it too appears to be an early off-shoot. Only one species, *S. loveridgei* is known in this group for which I propose the genus *Hyraconema* gen. nov.

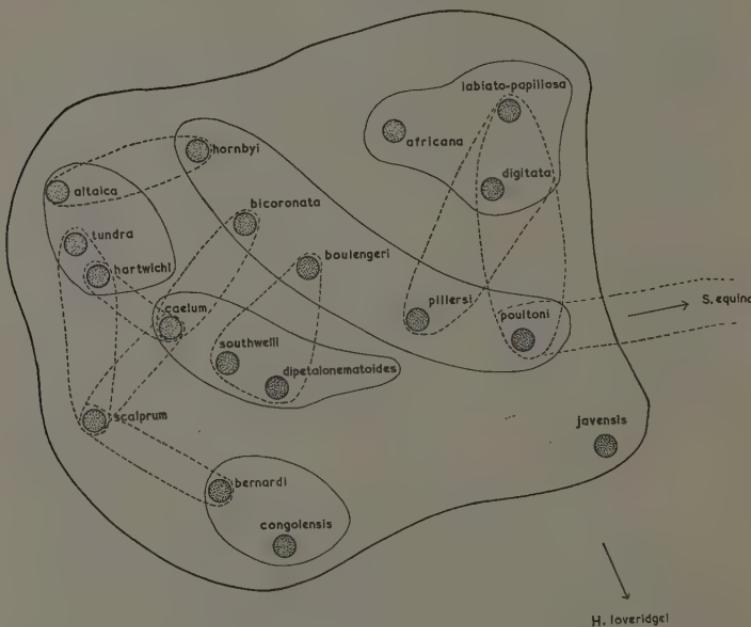


Fig. 185.—End on view of the phylogeny tree.

The remaining species are found in Artiodactyls. With the exception of the very primitive looking *javensis* which has a primitive buccal ring, and the male tail is partly with bosses and partly with rugae, they form a very homogeneous group. It is probable that *javensis*, like its host *Tragulus*, remained primitive while the others underwent further evolution together with their hosts. For this group of nematodes from artiodactyls, the name *Actionema* gen. nov. is proposed, with *A. africana* sp. nov. as genotype.

In the genus *Artionema*, *A. bernardi* and *A. congolensis* occur only in pigs. Three species which are known to occur in the Cervidae, appear to be specific to this host family. All the other species are distributed in four subfamilies of Bovidae, viz., Antilopinae, Cephalophinae, Hippotraginae and Bovinae.

All these parasites can be grouped in two ways—a horizontal or a vertical (=phylogenetic) grouping. A horizontal grouping would involve placing all parasites with similar morphological structures into species-groups or subgenera irrespective of their origin. Six groups could be distinguished in this way, viz : (a) those without elevations (*javensis* and *congolensis*), (b) those with four submedian elevations (*altaica*, *hornbyi*), (c) those with bifid elevations, (d) those with square elevations, (e) those with pointed elevations, and finally (f) those with lateral lips (*africana*, *digitata*, *labiato-papillosa* and *poultoni*). This appears morphologically good and sound, but, in fact, such a grouping is highly undesirable as the similarity of the morphological structures has resulted from convergent evolution, and at the same time it has no practical advantage over the vertical grouping.

The vertical grouping adopted here has much advantage. First, it shows the phylogenetic relationships of each of the parasites, and it is a practical system and easy to use for the identification of the species. A parasite like *A. altaica* in deer and *A. hornbyi* in the antelope would be grouped together in the horizontal system because of the similarity of the peribuccal ring. But as we have found, these parasites are very distantly related and should not be grouped together. We have shown earlier that in this group of parasites there has been a parallel evolution of host and parasite, and in the present instance it is undoubtedly advisable to use the host family grouping for parasites of Tragulidae, Suidae, Cervidae and subfamily groupings for worms from the Bovidae. Thus we achieve a natural vertical grouping which is practical and at the same time shows phylogenetic relationships. We have no doubt that it is the best system for the parasites in question. With our present knowledge of the group, it will be undesirable for us to group *A. hornbyi* and *A. altaica* together and to separate *A. hornbyi* and *A. bouleengeri* on morphological grounds.

THE SUBFAMILY SETARIINAE YORKE AND MAPLESTONE, 1926

Several classifications have been proposed for the Filarioidea, but none of them are satisfactory. Among these, the most practical and satisfactory is that proposed by Skrjabin and Shikhobalova (1945). In the family Setariidae Skrjabin and Shikhobalova, 1945, these authors recognised three subfamilies, viz : Setariinae Yorke and Maplestone, 1926, Dipetalonematinae Wehr, 1935, and Stephanofilaria Skrjabin and Shikhobalova, 1945. In the present communication, we are concerned with the subfamily Setariinae only.*

In the subfamily Setariinae, Skrjabin and Shikhobalova list *Setaria* Viborg, 1795 ; *Hyracofilaria* Ortlepp, 1937 ; *Ornithosetaria* Sandground, 1933 ; *Papillosetaria* Veyers, 1923 ; and *Skrjabinofilaria* Travassos, 1925. As *Hyracofilaria* is a synonym of *Filaria* Mueller, 1787, and *Ornithosetaria* is congeneric with *Politospiculum* Skrjabin, 1916, we are left with three genera in the subfamily Setariinae.

*It is a pleasure to note that there is now universal agreement on the recognition and definition of the subfamily Setariinae Yorke and Maplestone, 1926 and which genera should be included in it, with the publication of Chabaud and Anderson (1959) —*Nouvel essai de classification des filaires*. *Ann. Parasit. hum. comp.*, **34** (1/2), 64-87.

It is not my intention to go into the history of the superfamily and the various classifications, as I am dealing at the moment only with the subfamily Setariinae. This subfamily was proposed by Yorke and Maplestone, 1926, and recognized by Skrjabin and Shikhobalova (1936, 1945) but not accepted by Wehr (1935), Chabaud and Choquet (1953) and Lopez-Neyra (1956). The work of Skrjabin and Shikhobalova (1936) is in its essentials, rather similar to, and an improvement over Yorke and Maplestone (1926) : while Wehr (1935), on the other hand, uses larval characters and made many improvements over existing classifications, but the enumerated characters he used were more of theoretical interest than practical. Skrjabin and Shikhobalova (1945) revised their earlier classification and utilized some of Wehr's findings. Chabaud and Choquet (1953) following rather closely Wehr's system and backed by their extensive personal experience and studies, greatly improved on "Wehr's system". Lopez-Neyra (1956), in his compilation, closely followed Chabaud and Choquet. Now Chabaud and Anderson (1959) have realized the many drawbacks in the earlier paper by Chabaud and Choquet (1953) and have proposed a new classification, and in many instances, an entirely different system. In brief, the classification brings Wehr (1935), or Chitwood and Chitwood (1950), up-to-date. It is needless to say that there are many improvements over their older system (Chabaud and Choquet, 1953), but like it, there are many unacceptable proposals, as for instance, one wonders how Stephanofilaria and Setariinae can go together. Certainly, like the older system, a new essay will still have to follow. At least, now with their new paper (1959), and Skrjabin and Shikhobalova (1936, 1945), the validity of the subfamily Setariinae and the genera that should go with it are basically the same. This largely agrees with my present findings with the exception of *Skrjabinaria* Lubimov, 1927, which, according to my studies, certainly cannot be accepted in the subfamily Setariinae.

With our present revision of the genus *Setaria* s.l. we now recognise the following five genera in the subfamily Setariinae: *Skrjabinofilaria* Travassos, 1925; *Hyraconema* gen. nov.; *Setaria* Viborg, 1795; *Papillosetaria* Vevers, 1923*; and *Artionema* gen. nov.

Key to genera in the Subfamily Setariinae

1. Parasites of Marsupials..... *Skrjabinofilaria* Travassos, 1925
- Parasites of Hyracoids *Hyraconema* gen. nov.
- Parasites of Equine animals *Setaria* Viborg, 1795
- Parasites of Artiodactyls 2
2. Entire body with cuticular bosses..... *Papillosetaria* Vevers, 1923
- Body cuticle without bosses..... *Artionema* gen. nov.

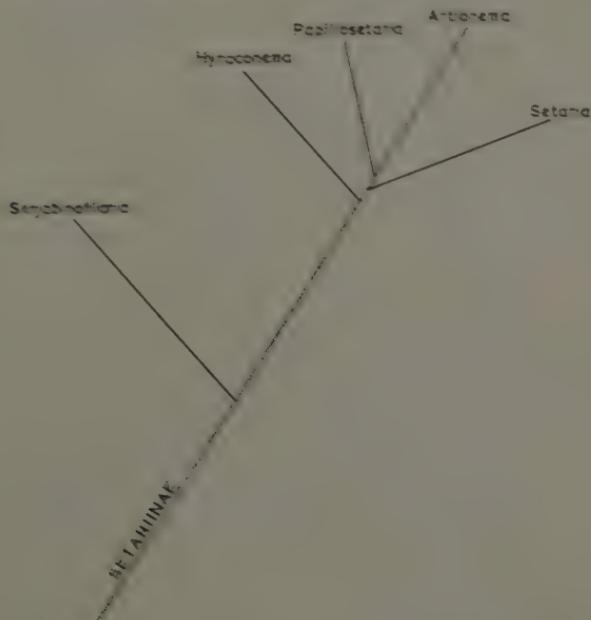


Fig. 186. The phylogeny of the genera in the subfamily Setariinae.

*The genus *Papillosetaria* by Vevers is usually incorrectly dated as 1922. As far as the date on the issue is 1922, this particular number was not published until early 1923. The correct designation is therefore *Papillosetaria* Vevers, 1923.

HOST LIST

HYRACOIDEA

PROCAVIIDAE

<i>Dendrohyrax</i> sp.	<i>Hyraconema loveridgei</i>
<i>Procavia brucei frommei</i>	<i>Hyraconema loveridgei</i>
<i>Procavia brucei prittwitzi</i>	<i>Hyraconema loveridgei</i>
<i>Procavia scheffleri</i>	<i>Hyraconema loveridgei</i>

PERISSODACTYLA

EQUIDAE

<i>Equus</i> spp. (Horse, donkey, zebra, mule) ...	<i>Setaria equina</i>
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ARTIODACTYLA

SUINAE

<i>Potamochoerus koiropotamus</i>	<i>Artionema congolensis</i>
<i>Potamochoerus porcus</i>	<i>Artionema congolensis</i>
<i>Sus cristatus</i>	<i>Artionema bernardi</i>
<i>Sus scrofa domestica</i>	<i>Artionema congolensis</i>
<i>Sus scrofa jubatus</i>	" <i>Setaria thomasi</i> " gen. et sp. <i>incertae sedis</i>

TRAGULIDAE

<i>Tragulus stanleyanus</i>	<i>Artionema javensis</i>
<i>Tragulus javanicus</i>	<i>Artionema javensis</i>

CERVIDAE

<i>Alces alces</i>	<i>Artionema altaica</i>
.....	<i>Artionema hartwichi</i>
<i>Capreolus capreolus</i>	<i>Artionema hartwichi</i>
<i>Cervus axis</i>	<i>Artionema altaica</i>
<i>Cervus canadensis asiaticus</i>	<i>Artionema altaica</i>
<i>Cervus elaphus</i>	<i>Artionema altaica</i>
<i>Moschus moschiferus</i>	<i>Artionema kabargi</i> (=? <i>A. tundra</i>)
.....	<i>Artionema kabargi</i> (=? <i>A. tundra</i>)
<i>Muntiacus muntjak</i>	<i>Artionema altaica</i>
<i>Odocoileus hemionus</i>	<i>Artionema tundra</i>
<i>Odocoileus virginianus</i>	<i>Artionema tundra</i>
<i>Rangifer tarandus</i>	<i>Artionema tundra</i>

BOVIDAE

ANTILOPINAE

<i>Aepyceros melampus</i>	<i>Artionema scalprum</i>
.....	<i>Artionema yorkei</i>
<i>Gazella granti</i>	<i>Artionema scalprum</i>
<i>Raphicerus campestris</i>	<i>Artionema scalprum</i>
<i>Ourebia kenyae</i>	<i>Artionema scalprum</i>

CEPHALOPHINAE

<i>Cephalophus dorsalis</i>	<i>Artionema caelum</i>
<i>Cephalophus melanorheus</i>	<i>Artionema caelum</i>
<i>Cephalophus maxwelli</i>	<i>Artionema caelum</i>
.....	<i>Artionema dipetalonematooides</i>
<i>Cephalophus sylvicultor</i>	<i>Artionema caelum</i>
<i>Cephalophus</i> sp.	<i>Artionema southwelli</i>

HIPPOTRAGINAE

<i>Alcelaphus lelwel</i>	<i>Artionema pouloni</i>
<i>Alcelaphus lichtensteini</i>	<i>Artionema hornbyi</i>
<i>Damaliscus corrigum jimela</i>	<i>Artionema pouloni</i>
<i>Damaliscus tiang</i>	<i>Artionema pouloni</i>
<i>Hippotragus equinus</i>	<i>Artionema hornbyi</i>
<i>Hippotragus niger</i>	<i>Artionema hornbyi</i>
<i>Kobus ellipsiprymnus</i>	? <i>Artionema hornbyi</i>
<i>Kobus kob</i>	<i>Artionema pillersi</i>
.....	<i>Artionema pouloni</i>
<i>Kobus leche</i>	<i>Artionema bicoronata</i>
.....	<i>Artionema bouleengeri</i>
<i>Kobus loderi</i>	<i>Artionema bicoronata</i>
<i>Kobus vardoni</i>	<i>Artionema bicoronata</i>
.....	<i>Artionema pillersi</i>
<i>Redunca arundinum</i>	<i>Artionema bicoronata</i>
.....	<i>Artionema bouleengeri</i>
<i>Redunca fulvorufula</i>	<i>Artionema bouleengeri</i>

BOVINAE

<i>Bos</i> spp.	<i>Artionema digitata</i>
.....	<i>Artionema labiato-papillosa</i>
<i>Bubalus</i> spp.	<i>Artionema digitata</i>
.....	<i>Artionema labiato-papillosa</i>
<i>Tragelaphus angasi</i>	<i>Artionema africana</i>
<i>Tragelaphus scriptus</i>	<i>Artionema yorkei</i>
<i>Tragelaphus sylvaticus</i>	<i>Artionema africana</i>

CAPRINAE

Sheep and goat *Artionema digitata* (abnormal host)

SUMMARY

In a revision of the genus *Setaria* s.l. the author gives a review of the literature on the systematics of this group. The genus *Setaria* s.l. is divided into three genera. *Hyraconema* n.g. monotypic for *H. loveridgei* (Sandground, 1928), a primitive worm of the hyracoids; *Setaria* Viborg, 1795, monotypic for *S. equina* (Abildg., 1789) the common parasite of equine animals; and *Artionema* n.g. for the remaining species, all of which occur in artiodactyls. *Artionema africana* n.sp. is the genotype. *A. africana* is found in *Tragelaphus* spp. and cattle in various parts of continental Africa. The other new species *A. hartwichi* n.sp. is found in the European deer, *Capreolus* and *Alces* on continental Europe. The paper includes a discussion on host parasite relationship, phylogeny and the evolution of taxonomic characters in speciation. In the Subfamily Setariinae Yorke and Maplestone, 1926, the author recognizes five genera as follows: *Skrjabinofilaria* Trav., 1925; *Hyraconema* gen. nov., *Setaria* Viborg, 1795, *Papillosetaria* Vevers, 1923 and *Artionema* gen. nov. The paper ends with a host list.

ACKNOWLEDGMENTS

I wish to thank Professor J. J. C. Buckley for his interest in the progress of my work and for many helpful suggestions and discussions, and to Dr. P. L. LeRoux for the privilege of examining his very extensive collection of worms and for his suggestions and discussions.

I am extremely grateful to very many colleagues who have been very helpful in many ways to make the investigation possible, especially to Dr. D. W. Amerasingha, Chief Municipal Veterinary Surgeon, Ceylon for collecting facilities; to Prof. Jean G. Baer, Université de Neuchâtel for information on European deer parasites; to Prof. P. L. G. Benoit, chef de la Section des Invertébrés, Musée Royal du Congo Belge, Tervuren, for the loan of type specimens of *Setaria rodhaini*; to Prof. Ettore Biocca, Direttore dell' Istituto di Parassitologia dell' Università di Roma for a collection of *A. labiatopapillosa*; to Prof. Thomas W. M. Cameron, MacDonald College of McGill University, Canada for photographs of deer *Setaria*; to Dr. Elisabeth Deichmann, Museum of Comparative Zoology at Harvard College, Massachusetts, for the loan of *Setaria loveridgei* type specimens; to Dr. J. A. Dinnik, East African Veterinary Research Organization, Kenya for specimens of *A. pillersi*; to Dr. A. S. Dissanaike, Department of Parasitology, University of Ceylon for collections of *A. digitata*, *A. labiatopapillosa* and blood smears;

to Dr. Robert Ph. Dollfus, Muséum National d'Histoire Naturelle, Paris for locating some type specimens; to Dr. J. F. B. Edeson, Institute of Medical Research, Malaya for collections of *A. javensis*; to Prof. R. M. Gordon, Liverpool School of Tropical Medicine for the loan of type specimens of *S. pouloni*, *S. boulengeri*, *S. yorkei*, *S. southwelli*, *S. pillersi* and other material; to Prof. J. Guilhon, Directeur du Laboratoire de Parasitologie, École Nationale Vétérinaire d'Alfort (Seine) for the loan of *S. congolensis* and *S. bernardi* type specimens; to Dr. G. Hartwich, Zoologisches Museum der Humboldt-Universität zu Berlin for the loan of von Linstow's types of *Filaria bicoronata*, *F. cornuta*, *F. scalprum*, *F. transverasta*, and specimens of *A. altaica* and *A. hartwichi* sp. nov.; to Dr. W. G. Inglis, British Museum (Nat. Hist.) for the loan of *S. sandersoni* and *S. southwelli* type specimens, and collections of *S. congolensis*, *S. pillersi*, *S. pouloni* and other material; to the Director, Evertebratavdelningen, Naturhistoriska Riksmuseum, Stockholm for the loan of *Filaria caelum* type specimens; to Dr. E. Kritscher, Naturhistorisches Museum, Wien for checking their type collections; to Dr. Allen McIntosh, Parasitologist in the Animal Disease and Parasite Research Division, Beltsville, Maryland for the loan of *A. tundra* specimens; and to Dr. P. Tate, Director of the Molteno Institute of Biology and Parasitology, University of Cambridge for giving a list of *Setaria s.l.* in their collection.

Finally I wish to express my gratitude to the very co-operative Library Staff of this School for assistance with the literature.

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Studies on *Anafilaroides rostratus* Gerichter, 1949 in Cats

I. The Adult and its first stage Larva*

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Anafilaroides rostratus Gerichter, 1949 has been recorded only from Palestine (Gerichter, 1949) and Ceylon (Seneviratna, 1955). Gerichter found it in one out of seventy-three cats examined; he had only a few specimens to describe and many of these were damaged. In Ceylon the extent of infection was heavy in the cats of the Kandy district where over 60% of the cats examined harboured the parasite, an amended description of which is given below.

ANAFILAROIDES ROSTRATUS Gerichter, 1949 :

Metastrongyloidea Lane, 1917 ; Filaroididae Schulz, 1951

The worms are long and slender, with a smooth integument. The female is milky white in colour with a dark brown intestine running through it. The anterior 3-6 mm. of the female is translucent; the rest of the body is milky white due to the presence of the uteri packed with embryos. The males are much smaller and dark brown in colour.

The anterior end has a protrusible rostrum (Figs. 1 and 2) which consists of six equal small lips arranged in pairs in close apposition. The buccal capsule has a triradiate opening formed by the three pairs of lips, one pair being disposed in each division formed by the Y-shaped opening. When the rostrum is retracted, the lips are not easily visible (Fig. 2) and in freshly fixed specimens 2-3 cuticular ridges may be seen at the anterior end. The cephalic papillae consist of four pairs of the external circle. These are the latero-dorsals and the latero-ventrals and the ventro-ventrals and the dorso-dorsals. The first two pairs of papillae are large and the other two pairs are much smaller (Fig. 3). The three pairs of the internal circle are rudimentary.

* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

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The oesophagus is club shaped and is retractile. It is very narrow anteriorly and bulbous posteriorly, the width of the bulb being about four times that of the anterior portion. The length of the oesophagus is variable according to the degree of protrusion or retraction of the rostrum.

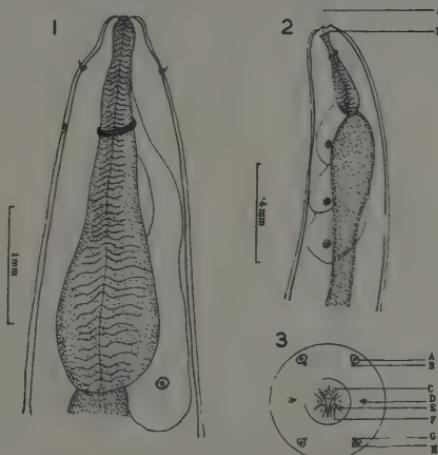
The Excretory System : A unique feature of these nematodes is that the excretory system opens near the anterior end ventrally and sub-terminally below and a little behind the oral opening. The opening is guarded by three unequal prominences, the two dorsal ones being smaller and the ventral one being larger. The excretory system consists of three unequal vesicles (Fig. 2) placed ventrally. Each of these vesicles has a large central excretory cell with a central nucleus that has much chromatin matter round its periphery. The largest vesicle in the female is about 0.65 mm. long while the others are up to 0.55 mm. and 0.22 mm. long respectively. The relative proportions of the excretory vesicles in the male are the same. The excretory duct is 0.1-0.12 mm. Each excretory vesicle is a saccular structure, broad behind and narrow anteriorly. The largest extends 0.24-0.3 mm. or more behind the terminal portion of the oesophagus. (Fig. 2.)

The Nervous System : The nerve ring is about 0.01 mm. thick and is situated about 0.1 mm. from the anterior end. The distance of the nerve ring from the anterior end varies according to the degree of protrusion of the rostrum.

Specific Diagnosis : (All measurements in millimetres).

Male—Length : 28-37, average : 35. Maximum width of body : 0.18-0.27. Oesophagus : 0.396-0.402 long, its maximum width is at its bulb and varies from 0.090-0.105. The oesophagus leads into a straight intestine packed with digested blood, dark brown in colour. The width of the intestine is 0.072-0.085. The posterior end of the worm is conical but bent slightly ventrally and lacks alae or caudal bursa. There are however four pairs of sessile post-anal papillae which decrease in size posteriorly. (Fig. 4). The spicules are sub-equal, slightly curved, stout, alate and measure 0.098-0.104; and 0.102-0.127 respectively. The maximum width of each is about 0.012. They are broad proximally and narrow distally. Three alae are present in each spicule, disposed in triradiate fashion. The gubernaculum is a slightly curved, irregularly pyramidal piece, 0.025-0.038 long. The tail is 0.078 long.

The female—The female measures 48–64 long with an average of 55·6. As it was impossible to remove the largest of the females without damage because they were firmly embedded in the peribronchial tissue and also surrounded by a fibrous tissue capsule, it is likely that the length given is an underestimate. The maximum thickness varies from 0·5–0·92 the mean being 0·72. The posterior end is 0·18 wide. The average length of the oesophagus is 0·375 with limits of 0·361–0·38 while the maximum breadth is 0·11 with limits of 0·10–0·13. The intestine is a simple straight tube.



Anafilaroides rostratus

Fig. 1.—Anterior end of male, dorsal view, with rostrum fully protruded. Note the relative position of the papillae to the rostrum when it is fully protruded.
 Fig. 2.—Anterior end of female, dorsal view with the rostrum completely retracted. A = Rostrum. B = Latero-dorsal papilla. Note the relative position of the papillae to the rostrum when it is completely retracted.

Fig. 3.—"En face" view of the anterior end, reconstructed from drawings of several preparations. Not to scale. A = Latero-dorsal papilla. B = Dorso-dorsal papilla. C = Lip. D = Amphid. E = Oral opening. F = Interno-ventral papilla (rudimentary). G = Ventro-ventral papilla. H = Latero-ventral papilla.

The female reproductive system was studied in worms recovered from the lungs, as well as in sections of lung tissue with the worms *in situ*. The female is opisthodelphic; one of the two ovaries arises in the middle of the posterior 5th of the body and runs forward in a tortuous manner gradually getting thicker. About 3–4 mm. from the anterior end it bulges to form a receptaculum seminis opening into a narrow tube, the oviduct, which turns backwards to form the

uterus. This is coiled either around the intestine or the other uterus and runs backwards in a tortuous manner. The second ovary arises in the middle of the anterior third of the body, runs backwards in a tortuous manner and, like the other one gives rise to the uterus about 15 mm. from the posterior end. The uterus runs forward to the middle of the anterior fourth of the body and back again to the posterior end in a tortuous manner.

The two uteri are packed with embryos in all stages of development and, in the distal portions, contain fully developed larvae surrounded by a very thin vitelline membrane. Sometimes a few free larvae are seen in the distal portions of the uteri.

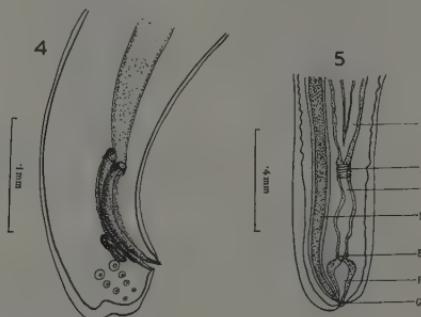


Fig. 4.—Posterior end of male, ventro-lateral view.

Fig. 5.—Posterior end of female, lateral view. **A**=Uterus. **B**=Uterine sphincter. **C**=Vagina. **D**=Intestine. **E**=Vaginal sphincter. **F**=Cloaca. **G**=Vulva.

The two uteri unite to form the vagina about 0.74 mm. from the posterior end of the body. The opening of the vagina into the two uterine tubes is guarded by a well developed vaginal sphincter 0.065 mm. thick (Fig. 5). The vagina is 0.5–0.54 mm. long and 0.07 mm. wide but the width varies according to the degree of distention with embryos. The vagina opens into a vulva which has a well developed ovejector. Near the junction of the vagina with the vulva is a weakly developed vulvar sphincter. The vulva opens near the posterior end close to the anus, both openings being in a common depression which is surrounded by three unequal flaps of which the ventral is larger and the other two of equal size. A true tail is absent but the larger flap, which extends 0.04 mm. from the common depression, may be referred to as the tail. The female is viviparous.

The first stage larvae. These are found in large numbers in the bronchi, trachea and the alimentary canal as they are coughed up, swallowed and passed in the faeces. Only on one occasion was it possible to collect a few larvae from the nasal mucosa.

The larvae in the lungs are shorter than those in the faeces (Table 1). Those in the faeces (Fig. 6) measure from 0·335–0·412 mm. long with an average of 0·367 mm. The maximum width which is in the region of the oesophageal bulb, is 0·018–0·02 mm. The oral opening is situated centrally and is surrounded by a cuticular ring with dorsal and ventral prominences (Fig. 7), a characteristic which distinguishes the species from the first stage larva of *Aelurostrongylus abstrusus*, another nematode found in the lungs of cats.

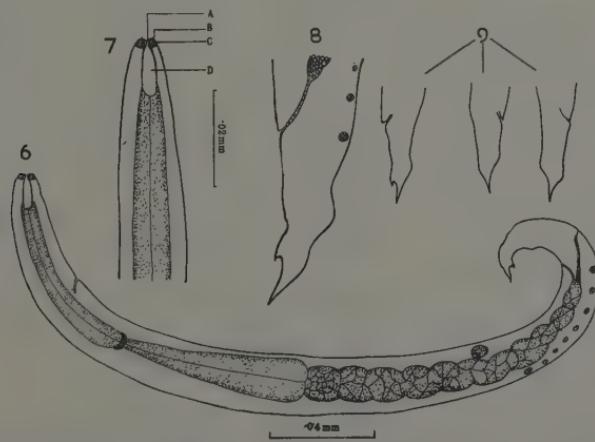


Fig. 6.—First stage larva, lateral view.

Fig. 7.—Anterior end of first stage larva, lateral view. Scale at right. A=Oral opening. B=Oral papilla. C=Cuticular ring. D=Buccal capsule.

Fig. 8.—Tail end of the first stage larva, lateral view. Note the hump on the dorsal side and the fine spine on the ventral side. Scale at left.

Fig. 9.—Variations in the appearance of the tail of the first stage larva.

The oral opening has six fine papillae and leads to an almost cylindrical buccal capsule, which is 0·009–0·010 mm. deep. The posterior portion of this capsule is inserted into the oesophagus which is 0·161–0·189 mm. long, with an average length of 0·163 mm.

The oesophageal bulb appears to be more or less truncate and is 0.012–0.014 mm. wide. The intestine which follows is thickly packed with dark granules. The tail is 0.036–0.039 mm. long and has a double undulation, usually with a spine on the ventral side (Fig. 8). The shape of the tail is however not constant, there being slight variations which are shown in Fig. 9.

TABLE I

Measurements in millimetres of the first stage larvae of *Anafilaroides rostratus*.

Character	Larvae found in fresh faeces	Larvae found in trachea	Gerichter, (1949)
Total length			
(a) variation	0.335–0.412	0.30–0.340	0.30–0.320
(b) average	0.367	0.320	
Maximum breadth	0.018–0.020	0.020	
Length of oesophagus			
(a) variation	0.161–0.189	0.140–0.170	0.150–0.160
(b) average	0.163	0.150	
Breadth of oesophageal bulb	0.012–0.014	0.018	
Distance of nerve ring from ant. end	0.080–0.095	0.078–0.082	
Distance of genital cell from ant. end	0.230–0.285	0.225–0.230	
Length of tail	0.034–0.039	0.032	0.031–0.035
Length of buccal capsule	0.009–0.010	0.010	0.010–0.012
Distance of excretory pore from ant. end	0.062–0.064		

The genital primordium is 0.23–0.285 mm. from the anterior end while the excretory pore is just posterior to the first quarter of the oesophagus, and is 0.062–0.064 mm. from the anterior end. The nerve ring is about 0.08–0.095 mm. from the anterior end surrounding a constriction on the middle of the oesophagus.

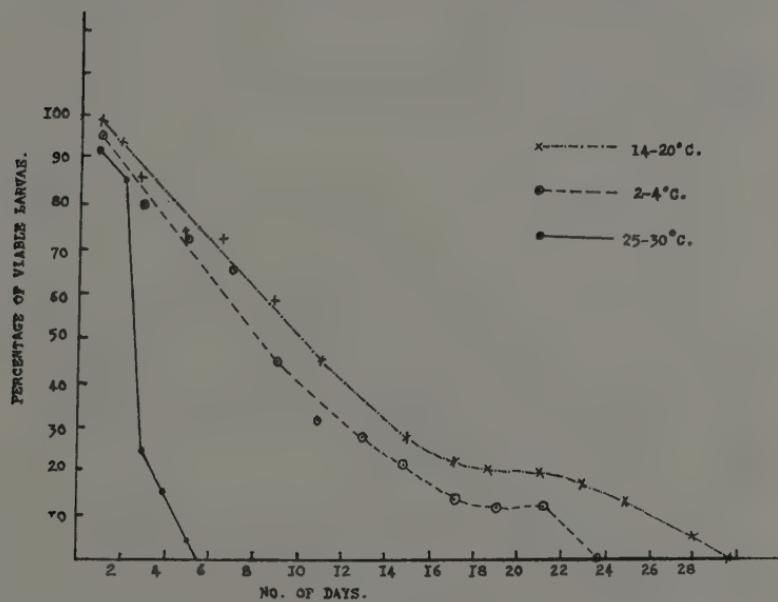
Homoeotype specimens: At the British Museum (N.H.), London and in the Department of Parasitology, Royal Veterinary College, London.

Host: Domestic cat, *Felis catus* Linné.

Location: Peribronchial tissue and bronchial wall.

Distribution: Palestine and Ceylon.

The biology of the first stage larvae of *A. rostratus* has not been studied before. Therefore the following data have been determined.



GRAPH I

The effect of temperature on the viability of the first stage larvae of *Anafilaroides rostratus* suspended in Baermann filtrate.

The viability of the larvae

It was found that the first stage larvae live in Baermann filtrate at 2-4°C. for 21 days, at 14-20°C. for 28 days, at 25-30°C. for 4-7 days and at 37°C. for 2 days only (see Graph I). Of the three media tested, viz.: distilled water, normal saline and Baermann filtrate, distilled water was the best medium for survival. Under natural

conditions at 26–31°C. in the Kandy district of Ceylon, live larvae were seen in a faecal sample after 73 days, though in several samples no larvae were seen many days earlier.

The larvae are very susceptible to the action of heat, for when subjected to 55°C. for one minute they were all dead. In this connection the thermal death point of a nematode larva may be defined and this is the lowest temperature above 37°C. at which all larvae die when exposed for one minute in suspension, in distilled water. This for the first stage larvae of *A. rostratus* is 55°C. The larvae are also susceptible to the action of cold, and overnight freezing kills them. Desiccation affects the larvae very adversely. In this connection the desiccation resistance index is defined for a nematode larva. It is the number of minutes taken by all larvae, suspended in distilled water, dried in a thin film on a glass slide, to die. In the case of *A. rostratus* first stage larvae this is five.

The effect of the following larvicides on the first stage larvae were studied : (1) lysol ; (2) copper sulphate ; (3) borax.

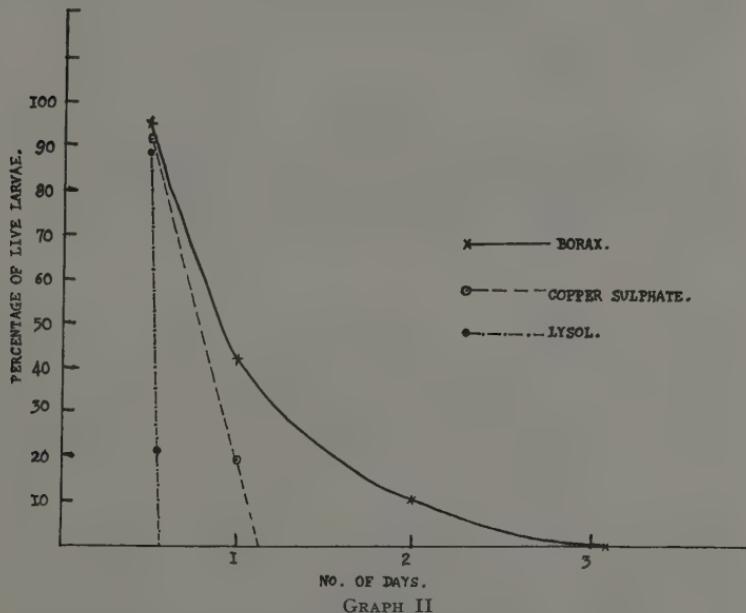
It was found that all these were detrimental to the larvae. Lysol was the most lethal and a 0·5% solution killed all larvae after 15 minutes. A similar strength of copper sulphate killed all larvae after 24 hours and a 1% solution of borax killed all larvae after 2 days (see Graph II). These experiments were done by adding aqueous solutions of the larvicides to suspensions of the larvae in Baermann filtrate, to obtain the required dilutions.

The larvae when tested with Goodey's cork raft technique (Goodey, 1922 and 1925) were unable to penetrate mammalian skin.

DISCUSSION

The present specimens resemble very closely those described by Gerichter (1949), except in a few details. Gerichter's specimens had a very undulating tegumental sheath. This was due to damage and this point has been verified with respect to the present material. Gerichter did not describe the excretory system. This is only seen in fresh undamaged specimens. No oral papillae were seen in the specimens from Palestine. The oral papillae are well seen only

when the rostrum is fully protruded. A complete study of these papillae can only be made from the "en face" view, which was not shown by Gerichter. The oesophagus of the male was shorter in Gerichter's material. It has been found that the length of the oesophagus varies with the degree of protrusion of the rostrum.



The effect of lysol, copper sulphate and borax on the first stage larvae of *Ana-filaroides rostratus* suspended in Baermann filtrate at 25–31°C.

The last point of difference is that the length of the gubernaculum is greater in the specimens from Palestine; but the writer has been unable to check this point. It is very likely that these few differences in the description given by Gerichter (1949) have chiefly been caused by the greater fragility of the worms, and the difficulty in obtaining specimens in reasonably good condition, from the peribronchial tissue in which they are embedded.

The first stage larvae as studied by Gerichter measured 0·3–0·32 mm. long whereas those in the present study measured 0·335–0·412 mm. long. Gerichter did not specify the site from which he

studied the larvae, but it is likely that they were from the lungs as he was at that time studying the lungworms of Felidae in Palestine. Further, his measurements support this view as the larvae found in the lungs by the writer measured 0·3–0·34 mm. There is therefore a distinct growth of the larvae during their passage in the faeces. A similar observation has been made with regard to a closely related nematode *Oslerus osleri* (Cobbold, 1879) by Urquhart, Jarret and O'Sullivan (1954).

SUMMARY

Anafilaroides rostratus Gerichter, 1949 a nematode found in the lungs of cats in Palestine and Ceylon, and its first stage larvae are described. Studies on the biology of the first stage larvae indicate that it is easily destroyed by adverse conditions.

ACKNOWLEDGMENTS

It is a pleasure to thank my Supervisor, Dr. J. N. Oldham, of the Royal Veterinary College, London, for his valuable suggestions and helpful criticisms given from time to time. Thanks are also due to Professor C. A. McGaughey, of the Ceylon University, and to the authorities of the Royal Veterinary College for the facilities provided in Ceylon and London respectively.

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ADDENDUM

- KLEWER (1958) has recorded this helminth from the bob cat, *Lynx rufus rufus* (Shreber) in Virginia.
KLEWER, H. L., 1958.—"The incidence of helminth lung parasites of *Lynx rufus rufus* (Shreber) and the life cycle of *Anafilaroides rostratus* (Gerichter), 1949". *J. Parasit.* **44** (4), Section 2, 29, (W.L. 11428).

+Studies on *Anafilaroides rostratus* Gerichter, 1949 in Cats

II. The Life Cycle*

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Gerichter (1949) found that there was slight development of the first stage larvae of *A. rostratus* when snails *Theba pisana* and *Monacha syriaca* were artificially infected. Larvae prior to the first moult were found after 26 days in *Theba pisana* at 4·8-12·5°C., and larvae in the same stage of development were found in *Monacha syriaca* after 36 days. He was unable to proceed with his experiments owing to lack of material and he did not consider the results conclusive.

Hobmaier, A. and Hobmaier, M. (1929 and 1930) were the first to indicate that certain lungworms of mammals used molluscs as intermediate hosts. Subsequently it was established that *Aelurostrongylus abstrusus*, another nematode found in the lungs of cats uses molluscs as intermediate hosts (Hobmaiers 1935a and 1935b). Except for the preliminary observations of Gerichter (1949) the life history of *A. rostratus* has not been studied before.

† Since this paper was sent to press, Klewer (1958) has found that *Lynx rufus rufus* (Shreber) the bob cat from Virginia is also a host for *A. rostratus*. Twenty three of the twenty four cats examined harboured the adult parasite. Under laboratory conditions the slug *Limax maximus* was found to act as the intermediate host. Two moults were found to occur in the foot muscle of the slug within ten days and infective larvae without any sheath were found on the 11th day. Experimental infection was carried out in domestic kittens.

Reference : Klewer, H. L. (1958) : "The incidence of helminth lung parasites of *Lynx rufus rufus* (Shreber) and the life cycle of *Anafilaroides rostratus* (Gerichter), 1949. *J. Parasit.* **44** (4), Section 2, 29, (Abstract 54). (W.L. 11428).

THE DEVELOPMENT IN MOLLUSCS

Material and Methods : The first stage larvae of *A. rostratus* were separated by the Baermann technique, from fresh cat faeces, and snails and slugs were allowed to move in the fluid rich with larvae for 5 to 15 minutes by placing them in a Petri dish containing the larval suspension.

* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

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The following molluscs were used in the experiments :—

(A) Molluscs from Ceylon :—

(1) Snails : *Achatina fulica* (Fer.), *Opeas (Bulimus) gracile* Hutton and *Opeas prestoni* Sykes.

(2) Slugs : *Mariella dussumieri* Gray, and *Laevicaulis alte* Fer.

(B) Molluscs from England :—

(1) Snails : *Helix aspersa* Müller and *Cepea hortensis* Müller.

(2) Slugs : *Trichia striolata* (Pfeiffer), *Agriolimax reticulatus* (Müller) and *Milax budapestensis* (Hazay).

(C) African molluscs : *Archachatina marginata* (Swainson), one only.

After infection these molluscs were transferred to boxes, half filled with earth. Each box was divided into two unequal compartments. The molluscs used for infection were placed in the larger compartments while the control molluscs were placed in the smaller ones. A few infected molluscs were examined half an hour after infection trials while the others were examined at intervals varying from 24 hours to 60 days. The results are recorded in the table below. Except for the molluscs killed 30 minutes after infection, the others were drowned in boiled cooled water and dissected, the foot and the body being examined separately. In some molluscs the foot was cut off, fixed in 10% formol saline, sectioned and examined. For the study of the larval stages it was found that the dissection of the drowned snails or slugs gave better results than the cutting of sections.

It was found that nearly all the *Achatina fulica*, *Mariella dussumieri* and *Laevicaulis alte* were infected, while the percentage of infected *Helix aspersa* was about 75, and that to infect molluscs in England, it was necessary to heat the larval suspension to about 25°C. *Laevicaulis alte* was used to study the details of larval development in Ceylon as this was the commonest slug available in the Kandy district and the easiest to dissect. *Helix aspersa* was used to study the larval development in England as this was the only mollusc that could be infected in this country.

Of the molluscs used above, the following were successfully infected :—

1. *Laevicaulis alte* Fer.
2. *Mariella dussumieri* Gray.
3. *Achatina fulica* (Fer.)
4. *Helix aspersa* Müller.

The rates of development of *A. rostratus* in the different species of molluscs at the various temperatures at which they were reared, varied considerably and are given below

Rate of development of A. rostratus in molluscs at 24–30°C.

Species of mollusc.	First moult completed	Second moult completed
<i>Achatina fulica</i>	14 days	22 days
<i>Laevicaulis alte</i>	14 days	20 days
<i>Mariella dussumieri</i>	18 days	28 days

Rate of development of A. rostratus in Helix aspersa.

Temperature	9.5–21.5°C.	24°C.
First moult	38 days	18 days
Second moult	56 days	26 days

Details of development, at 24–30°C.: The first stage larvae of *A. rostratus* penetrate the foot of the snail through the mucous glands, and the molluscs show no evidence of any inconvenience due to penetration. Many of the larvae appear to become very active when the molluscs are placed in the fluid containing them. Many become entangled in the mucous secretions and this facilitates penetration, although the exact method of penetration could not be observed.

The first stage larvae in the molluscs: After penetration, the larvae wander in the foot but do not encyst. They feed and grow and on dissection all larvae are seen to be very active. In *L. alte*, on the 7th day the average measurements in microns of the larva is as follows : Length of body 390, breadth 26, length of oesophagus 160, length of tail 36, distance of excretory pore from anterior end 60, (Fig. 2). There is no marked increase in the length but there is an appreciable increase in the thickness of the body. From the 7th day onwards, activity decreases, the body becomes darker due to the deposition of food granules and there is an overall increase

in the body size. Just before the first moult, the larva becomes completely quiescent. The various stages in the mollusc are illustrated in Figs. 2-8 and in Plate 1, and their measurements and characters given in Table 1.

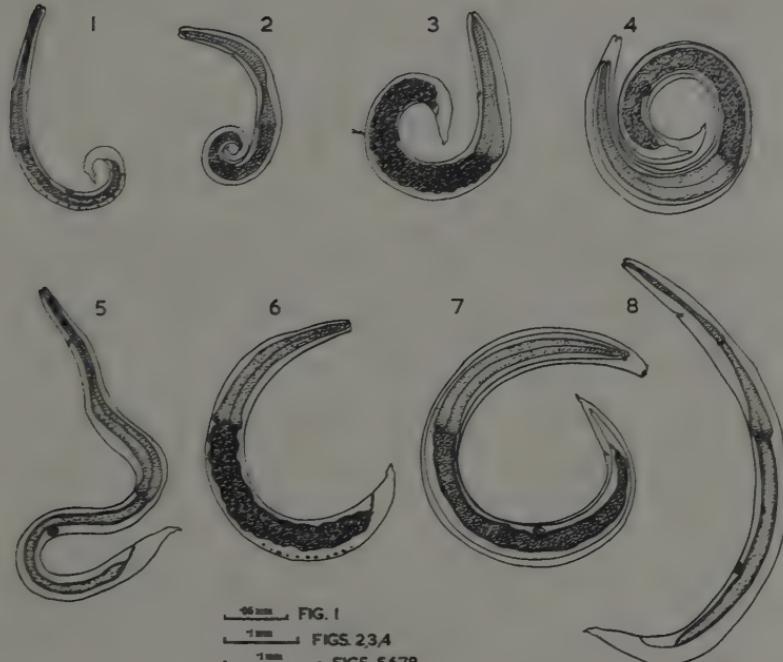
TABLE 1

Measurements (in microns) and characters of the larvae of *Anafilaroides rostratus* in *Laevicaulis alte* at 24-30°C.

	1st stage larva after 7 days	1st stage larva before 1st moult, after 12 days			After 1st moult at 16-18 days	After 2nd moult at 26 days
Total length	390	465	580	620-700		
Max. breadth	28	40	38	36		
Length of oesophagus	160	160	240	240		
Breadth of oesophagus at bulb		25	25	20		
Distance of excretory pore from ant. end	60	86		75		
Distance of genital cell from ant. end		310	350	395		
Length of tail	36	40	35	60		
Length of buccal cap- sule	...		10	13		
Character of buccal capsule	Cylindrical	Oval	Oval	Beak shaped		
Character of tail	Kink	Kink	Beak shaped	Beak shaped		
Granules	Increase of granules	Marked increase of granules	No granules	No granules	

The second stage larvae: The first moult is generally completed in *L. alte* in 13-14 days. The cuticle is then shed and the larva becomes active, feeds and grows, there being a marked increase in the length and breadth. On about the 18th day the larva is in preparation for the second moult and by the 20th day this has been completed.

Third stage infective larvae. After the second moult the cuticle is cast off leaving the larva free (Fig. 8). It is about 620-700 μ long and 36 μ broad in the region of the oesophagus. Other average measurements are: Length of oesophagus 240 μ , breadth of oesophagus at bulb 20 μ , length of tail 60 μ , distance of excretory pore from anterior end 75 μ , distance of genital cell from anterior end 395 μ . (See Table 1).



Anafilaroides rostratus, larval stages

Fig. 1.—First stage larva as found in faeces. Fig. 2.—First stage larva as found in the foot of mollusc, *Laevicaulis alte*, 7 days after penetration. The larva has grown in width but there is no appreciable increase in the length. The intestine is gradually loaded with food material. Fig. 3.—First stage larva just before the start of the first moult. It is inactive and the intestine is loaded with food material. Fig. 4.—The completion of the first moult. The cuticle is separated but is still not shed. The food material is partly used up. Fig. 5.—Second stage larva after the cuticle is shed. Fig. 6.—Second stage larva just before the second moult. The buccal capsule is everted and the intestine is loaded with food granules. Fig. 7.—Completion of the second moult. The cuticle is separated but still not shed. Fig. 8.—Infective third stage larva in the foot of *Laevicaulis alte* after 24 days at 24–30°C., lateral view. Note the anterior cuticular thickening and the beak like tail.

The rate of development. The rate of development is affected considerably by the environmental temperature. It was found that during December and January, when the laboratory temperature in Ceylon was from 23.4-29°C., all larvae reached the infective stage in *L. atra* after 28-29 days, whereas during March, April and May, when the laboratory temperature varied from 26.4-32.8°C., all larvae reached the infective stage in 18-19 days in *L. atra*. In the experiments with *H. aspersa* in England, the larvae reached the infective stage in 26 days at 24°C. while they took 56 days to reach this stage at 9.5-21.5°C.

The site of development. The larvae develop only in the foot of the molluscs. After development, the majority remain in the foot but a few migrate to the body and may be found in the lungs, liver and the alimentary canal of the snails and slugs. Groups of *A. fulica* and *L. atra* examined after 43 days and 52 days respectively, showed that the majority of the larvae were still in the foot.

The characteristics of the larvae during the various stages of development. During these experiments it was noticed that as many as 60% of the slugs and snails from Ceylon and a much smaller percentage of the molluscs from England harboured adult soil nematodes and many other larval nematodes in the body but rarely in the foot. The gross size of these larvae enabled them to be differentiated from those of *A. rostratus*. The following characteristics also enabled the larvae of *A. rostratus* to be distinguished from those of the other nematodes. 1) The gross size. (Given in the tables). 2) The characteristic kink in the tail which was maintained throughout the larval development, although the irregularities gradually decreased and the infective larval stage had a beak-like process preceded by a thumb-like prominence. 3) The relative length of the oesophagus which in the first stage larva, was a little less than half the length of the body, but in the infective stage was a little more than one-third the length of the body. 4) The buccal capsule was represented by a narrow slit in the first stage larva and as the larva developed it became oval while just prior to the second instar, there was an eversion of the buccal capsule. In view of the general uniformity of the character of the larva and its gradual changes there was no possibility of confusing it with any other larvae seen in the molluscs.

After penetrating the foot of the mollusc, the first stage larva feeds and becomes very active, maximum activity being reached

about the 7th day, when its body is clear and translucent. After this the body becomes darker and broader and about the 12th day the larva becomes non-motile and the first moult is completed after the 14th day. Following this moult the cuticle is shed, the body becomes clear, and the larva becomes active again. This phase lasts only a few days. About the 18th day it again becomes lethargic and the body becomes loaded with food granules. The second moult occurs about the 20-22nd day. After this the larva sheds its cuticle and becomes active and infective. These changes take place in *A. fulica* and *L. alte* at 24-30°C.

Natural infection in molluscs. When the experiments involving the life history were being conducted, many snails and slugs viz. *A. fulica*, *M. duosumieri* and *L. alte* were collected in the area surrounding the laboratory in Peradeniya, Ceylon. The foot of over 100 of these was examined and in only two specimens of *L. alte* were infective larvae of *A. rostratus* seen; in both cases, there were two or three larvae in the foot. Later, batches of snails and slugs were drowned, their foot cut off, dissected, and placed in the Baermann apparatus. In two out of ten batches examined, several larvae of *A. rostratus* were seen. All were in the infective stage.

It was of interest to note that, even though the incidence of natural infection was low in snails and slugs and that cats rarely ate them, the infection of the cats with the adult nematodes was very heavy. It was thought that this was due to two factors: (1) The great abundance of slugs and snails in the Kandy district where, literally thousands of them may be seen in the morning on a moist day on an acre of land, and (2) the use of auxiliary hosts by the infective larvae as is the case of other nematodes such as *A. abstrusus*, and *S. lupi*.

THE AUXILIARY HOSTS

Cameron (1926, 1927b) found that the third stage larvae of *Aelurostrongylus abstrusus* occurred in mice and he, erroneously, concluded that mice were the intermediate hosts. Later M., and A. Hobmaier (1935c) showed that mice really acted as auxiliary hosts and that the true intermediate hosts were molluscs, (Hobmaierns, 1935a and 1935b) and that rodents, frogs, toads, lizards, snakes, birds, chickens and ducklings could act as auxiliary hosts (Hobmaierns 1935c).

The role of mice. Experiments in Ceylon. Three white mice (a, b and c), about four weeks old, were each given 200-400 infective larvae of *A. rostratus* which were obtained from the foot of molluscs by separation in the Baermann apparatus. The larvae were given orally by a one foot long piece of polythene tubing used as a stomach tube, after anaesthetising the mice with ether. A fourth mouse (d) acted as control. The mice were examined after 30-40 days, when third stage unencysted larvae were seen in the intercostal and thoracic muscles and diaphragm in mouse (A), and in the sub-lumbar muscles in mouse (B). No larvae were seen in the other mice. The larvae were not visible to the naked eye, but their location was marked by fine, white, pin-point spots. These larvae from the mice, were given to two cats, on 26th May, 1955, and several ovigerous *A. rostratus* were seen in the lungs of one after 85 days but not in the other.

Experiments in England. Four white mice, about four weeks old, were each given about 30 infective larvae of *A. rostratus* on 26th July, 1956. One mouse died the same day. Two of the remaining mice were killed and fed to a cat on 4th August, 1956. The fourth mouse was killed on 6th August 1956 its body digested, and several infective larvae were recovered from it. On 24th January, 1957, this cat was killed and was negative. In these experiments, only about 30 infective larvae were given to each mouse as numerous larvae were not available for experimental purposes since the number of infective larvae recovered from *H. aspersa* in England was small. It is probable that the small number of larvae fed to the mice failed to infect the cat.

The successful infection of one cat proved that mice can act as auxiliary hosts, even though the other cats were negative.

The role of chickens. Experiments in Ceylon. Four seven day old chickens, numbered 1, 2, 3 and 4, were each given the chopped up foot of *Achatina fulica* and it was roughly estimated that each received about 80 third stage larvae of *A. rostratus*. Two more chickens, No. 5 and 6, acted as controls. The chickens were killed 40 days later and their carcases examined. Chickens No. 3 and 4 showed the presence of third stage larvae, two being recovered from the crop of chicken No. 3; and 5, of which two were in the crop and three in the mesentery from chicken No. 4. No larvae were seen in the other chickens. Feeding experiments with cats were not done as the writer was to leave for England.

Experiments in England. Three 7 day old chickens (R.I.R.), E1, E2 and E3, were fed on 26th July, 1956 with the infected foot of *H. aspersa* each chicken receiving approximately 75–150 third stage larvae of *A. rostratus*. Chickens E1 and E2 were killed after one week and were fed to a cat on 4th August, 1956. The carcase of the third chick, that died one week later, was artificially digested and the residue examined for the presence of larvae but none was seen. On 24th January, 1957 the cat was killed and live adults of *A. rostratus* were seen in the lungs at examination *post mortem*.

The role of auxiliary hosts under natural conditions. Ten domestic rats were caught in Ceylon at various intervals and examined for the presence of third stage larvae of *A. rostratus*. One showed third stage larvae in the diaphragm but no feeding trials with cats were done. Besides rats, the crow pheasant, *Centropus sinensis paroti*, which is commonly found in Ceylon, is a voracious feeder on snails and could possibly act as an important auxiliary host. It was impossible to verify this as it is a protected bird.

THE DEVELOPMENT OF *Anaflaroides rostratus* IN CATS

Material and Methods in Cats. The development of *A. rostratus* was studied by feeding third stage infective larvae, obtained from experimentally infected molluscs, to kittens kept in the laboratory. The kittens, in most of the experiments, were 4–6 weeks old and in each batch there were 3–5 animals usually from the same litter. The previous history was ascertained in every case when it was found that they had had no opportunity to stray out for food or have access to snails, slugs or the auxiliary hosts. If there was no such history the kittens were rejected. In the experiments conducted in England, where *A. rostratus* does not exist the kittens were two to three months old farm animals. In each batch, one or two kittens acted as controls. It was very important to have controls in Ceylon experiments as the infection under natural conditions was common. The infective material in each of the experiments was either (1) the infective third stage larvae, free of any sheath, recovered from molluscan foot by the Baermann technique; (2) the foot of molluscs containing the infective material; or (3) in a few instances the auxiliary hosts that were experimentally infected with third stage larvae. Wherever possible after experimental infection, the cat faeces were examined at weekly or fortnightly intervals by the Baermann technique for the presence of first stage larvae.

The route of penetration and the further development of the third stage larvae recovered from molluscs were studied in kittens listed in Table II.

The infective larvae, after ingestion, penetrate the stomach wall as was proved in cat No. 6 where three larvae were found in the stomach wall twenty-four hours after infection. The route taken by them thereafter is not certain though attempts to study this were made in cats No. 6, 7 and 47. Probably they reach the predilection site through the lymph stream, as in the case with some other lungworms.

The blood from cat No. 6 was examined for the presence of the larvae but none was found. These negative results however are not conclusive as only 50 infective larvae were used in the feeding. The limited number of infective larvae available was a disadvantage throughout the study of development in the definitive host as it was difficult to trace the course of migration or the site of localisation of the larvae when small numbers were used.

Cat No. 6 given 50 infective larvae orally, did not show any larvae in the lungs or any other organs, but three larvae were seen in the stomach wall which they had apparently penetrated. Cat No. 7, given about 50 infective larvae, was negative after three days while cat No. 8 given about 90 infective larvae, showed after 5 days larvae in the lungs by the Baermann technique although no larvae were seen in the other organs. These larvae from the lungs appeared to be fourth stage larvae just after the completion of the third moult. One complete specimen measured 1.2 mm. long and 0.05 mm. wide. The oesophagus was shorter than that of the infective larva and was bulbous consisting of a procorpus, mesocorpus and metacorpus. The oral opening was a narrow slit which led into an insignificant buccal capsule. The tail was longer than that of the infective larva, not kinked but straight, and truncate at the tip. Cat No. 9 given about 50 infective larvae, was negative after 6 days and cat No. 47, given about 250 infective larvae, was negative after 8 days. This cat (No. 47) vomited after the infective larvae were given but part of the vomitus was fed to it again. Cat No. 11, given about 50 infective larvae, showed the presence of a larval helminth, probably the fourth stage larva of *A. rostratus*, in sections of the lung, after 19 days. Cat No. 48 showed fourth stage larvae just before the commencement of the fourth moult, 24 days after infection. Cat No. 13, given about 50 infective larvae, showed immature helminths in the lungs after 46 days on histological examination, and cat No. 15 showed several immature females and one immature male after 56 days. These were dissected out, studied and identified as *A. rostratus*. The undamaged female was 3.5 cms. and the male 2.1 cms. long. The general structure was the same as in the adult nematode but the ova had not developed. Cat No. 16 also harboured non-gravid *A. rostratus* after 58 days and in this case only females

Summary of the results in some of the experimental cats used in the study of development.

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No. of cat	No. of infective larvae fed	Days before euthanasia	Result	Stage of development of worm and organ in which it was seen	Organs examined and techniques employed to detect infection
6	50	1	Positive	3rd stage larvae in stomach wall	Microscopic examination
7	50	3	Negative		Lungs, liver and alimentary canal, histologically, microscopically and by Baermann technique
8	90	5	Positive	Probably 4th stage larvae in the lungs	By Baermann technique
9	50	6	Negative		All techniques as in cat No. 7 and also digestion
11	50	19	Positive	Probably 4th stage larvae in the lungs	Histologically
13	50	46	Positive	Immature helminths in the lungs	Histologically
15	100	56	Positive	Immature helminths in the lungs	Macroscopically, histologically and by dissection
16	100	58	Positive	Non gravid females in the lungs	Dissection and histological examination
42	130	313	Positive	Live adults in the lungs	Macroscopically
43	50	74	Positive	Gravid females in the lungs	Macroscopically and by dissection
44	25	69	Negative		All techniques
45B	100	145	Negative		All techniques
46	120	140	Positive	Adults in the lungs	By digestion
47	250	8	Negative		Portions of lung, liver, brain, spleen and alimentary canal examined by Baermann technique, macroscopically, histologically and by digestion
48	125	24	Positive	Probably 4th stage larvae in the lungs	Histologically

were seen. Cat No. 42, fed about 130 infected larvae started excreting first stage larvae after 78 days, and live adults were seen on euthanasia after 313 days. Cat No. 43 showed adult helminths 74 days after feeding the infective larvae. Cat No. 44 and 45B were negative after 69 and 145 days respectively. Cat No. 46 was found to harbour adult helminths 140 days after infection.

DISCUSSION

It has been established that the development of the larvae of *A. rostratus* occurs in molluscs, and this has also been proved for other related species such as *Aelurostrongylus abstrusus* by the Hobmaiers (1935a and 1935b) for *Aelurostrongylus falciformis* by Wetzel (1937) and for *Filaroides martis* by Petrov and Gagarin (1937).

In all these parasites two moults occur in the mollusc and the infective larva retains either one or two sheaths which easily become detached. The present observations on *A. rostratus* are at variance with this for in no case does the infective larva retain its sheath. After each moult the cuticle is shed. It is unlikely that the cuticle was shed as a result of manipulation, because the infective larvae, separated by the Baermann technique, did not have any sheath. This indicates that *A. rostratus*, though related to the other nematodes mentioned earlier, has marked distinctions from them and that Dougherty's assumption (Dougherty, 1951) that *Anafilaroides* is synonymous with *Filaroides* is open to question. The only member of the genus *Filaroides*, the life history of which is known is *F. martis*, which has been traced by Petrov and Gagarin (1937) and the differences in the details in the life history indicate that the generic distinction of *Anafilaroides* would be justified.

Gerichter (1948 and 1951) concluded that the life history of Metastrongylids involved the occurrence of two moults and that there were four stages in the mollusc. He considered that there were two stages after the second moult, the pre-infective stage and the infective stage. In the case of *A. rostratus* the writer is unable to substantiate this statement. Two moults appear in the mollusc, but there appear to be only three stages. It is likely that a period of maturation is necessary after the second moult for the larva to become infective, but to conclude that a process of maturation leads to a fourth stage is erroneous, since it is usual to designate the larva after each moult as a separate stage.

Experiments with mice and chickens prove that they can act as auxiliary or transport hosts although it was impossible to demonstrate the third stage larvae in every case when they had been fed

to the auxiliary hosts. It is unlikely that the experimental Ceylonese cats were naturally infected and such an assumption is impossible in the case of the cat fed in England, since this animal was born and bred in England, where infection with *A. rostratus* does not exist.

Though feeding experiments were not done with the larvae recovered from the rat it is very likely that they were those of *A. rostratus*, even though they also resembled the third stage larvae *Aelurostrongylus abstrusus*, which as far as our present knowledge goes, does not exist in Ceylon. In view of the observations that cats rarely eat snails even if they are very hungry it is very likely that these auxiliary hosts, rats, chickens and very probably other rodents and birds or even lizards may play a very important part in the infection of the cats.

Observations on the development in cats were greatly handicapped by the lack of suitable infective material and therefore are incomplete. To study the complete development in cats very large numbers of infective larvae and many experimental cats would have been required, but neither was available at the time this work was done. Though the British mollusc, *H. aspersa*, could be infected, the number of larvae that developed in its foot was small, so that the feeding experiments in England were limited.

SUMMARY

The first stage larva of *Anafilaroides rostratus* develops, after penetration into the foot of certain molluscs, *Laevicaulis alte* Fer., *Mariella dussumieri* Gray, *Achatina fulica* (Fer.) and *Helix aspersa* Müller. Two moults occur in the foot of these molluscs in 20–56 days depending on the temperature. After each moult the cuticle is shed. The details of development are described. The infective larvae are found in the foot of these molluscs. Natural infection was found in *L. alte*.

Mice and chickens can act as auxiliary hosts. Probably rats, other rodents and birds can also act in the same capacity.

The study of the development of the parasite in the cats is not complete. On ingestion the infective larvae penetrate the stomach wall and reach the lung where the third and the fourth moults occur. Exact times of the occurrence of the moults have not been definitely established. All moults are however completed by the 46th day; from then until the 58th day, immature helminths are found in the lungs. Fully gravid females are found on the 74th day, and larvae are first seen on the 78th day. The worms continue

to produce larvae for more than 255 days after maturity. The duration of the life of the adult is probably considerably longer than one year.

ACKNOWLEDGMENTS

It is a pleasure to thank my Supervisor Dr. J. N. Oldham, of the Royal Veterinary College, London, for his valuable suggestions and helpful criticism given from time to time. Thanks are also due to Professor C. A. McGaughey, of the Ceylon University, and the Authorities of the Royal Veterinary College, London for the facilities provided in Ceylon and London respectively; to Dr. H. C. Ray of the Zoological Survey of India, for identifying the molluscs from Ceylon; to Mr. I. C. Galbraith, of the British Museum (Natural History) for identifying the molluscs from England.

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ADDENDUM

KLEWER (1958) has observed that the infective stage of *A. rostratus* was reached in the slug *Limax maximus* in 11 days and that this stage was devoid of sheath.

KLEWER, H. L., 1958. "The incidence of helminth lung parasites of *Lynx rufus rufus* (Shreiber) and the life cycle of *Anafilaroides rostratus* Gerichter, 1949". *J. Parasit.*, **44** (4), Section 2, 29. (W.L. 11428.)

Studies on the Family Filaroididae Schulz, 1951*

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The systematic position of certain lungworms of mammals that have either a reduced bursa, or no bursa, has been in considerable doubt for some time. Thus, Cobbold (1879) recognized Filariid affinities in *Oslerus osleri* (Cobbold, 1879), a lungworm without a caudal bursa, found in dogs. Yorke and Maplestone (1926) placed the genus *Filaroides* v. Beneden, 1858 in an uncertain position close to the Filarioidea, while Baylis and Daubney (1926) placed it in the Metastrongylidae.

Skrjabin (1933) erected the subfamily Filaroidinae to accommodate the genus *Filaroides* and placed his subfamily in the Pseudaliidae Railliet, 1916 implying thereby the close association of the genus with the Pseudalian lungworms. However, certain helminthologists, Dougherty (1943 and 1946) and Chitwood & Chitwood (1950) placed the Filaroidinae in the Metastrongylidae. All these authors admitted that this system of classification was unsatisfactory.

After the erection of the family Filaroididae Schulz, 1951, the classification of this group of nematodes has become more satisfactory. However, Schulz neither defined the family nor the several subfamilies that he erected in his paper. In the same paper he erected the genus *Angiocaulus* to include *Angiostrongylus gubernaculatus* Dougherty, 1946. There seems to be no justification for the erection of this genus as *A. gubernaculatus* does not appear to differ from the other members of the genus *Angiostrongylus* Kamensky, 1905, which have been studied and listed by Dougherty (1946), except for the presence of a gubernaculum and slightly shorter dorso-dorsal rays. Hence *Angiocaulus* may be regarded as a synonym of *Angiostrongylus*. The second genus that Schulz erected in the same paper was *Rattostrongylus* to include *Angiostrongylus cantonensis* (Chen, 1935) Dougherty, 1946. Chen described this nematode under the name *Pulmonema cantonensis*. It differs from the other members of the genus *Angiostrongylus*, only in the greater length of the spicules. However, the length of the spicules of the

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various races of this nematode found in Australia is variable (Mackerras, 1957), so that this character has little validity in this respect. The genus *Pulmonema* was reduced to a synonym of *Angiostrongylus* by Dougherty (1946), but should a generic separation later become necessary, *Pulmonema* has priority over *Rattostrongylus* as the name *Pulmonema* is not preoccupied (Neave, 1940).

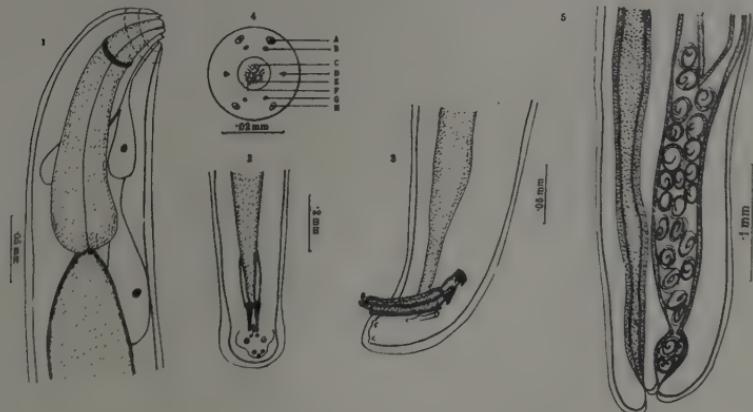
Skrjabin *et al.* (1952) have defined the family Filaroididae and listed the genera and species in it. However, morphological data on some genera and species of this family were inadequate. Detailed studies of them have been handicapped by their great fragility and their location in the blood vessels of the lung, making their separation from the tissues in reasonably good form rather difficult. None of the previous workers on the systematics of this group studied the specimens in detail.

In the present study the following specimens obtained from the sources mentioned were examined :—

- A. Specimens from the British Museum, (Nat. Hist.) :
 - 1. *Filaroides martis* (Werner, 1782) Dougherty, 1943.
 - 2. *Skrjabingylus nasicola* (Leuckart, 1842) Petrov, 1927.
 - 3. *Pseudalium inflexus* (Rudolphi, 1809) Schneider, 1866.
 - 4. *Vogeloides oesophageus* (Gerichter, 1948) *emend. nov.*
 - 5. *Pneumospirura capsulata* (Gerichter, 1948) Dougherty, 1952.
 - 6. *Metathelazia multipapillata* Gerichter, 1948.
 - 7. *Halocercus invaginatus* Quekett, 1841.
- B. Specimens from the Royal Veterinary College, London :
 - 1. *Oslerus osleri* (Cobbold, 1879) Hall, 1921.
 - 2. *Parafilaroides decorus* Dougherty and Herman, 1947.
- C. Specimens from other sources :
 - 1. *Oslerus kreisi* (Dougherty, 1943) *comb. nov.*; from the Natural History Museum, Basle.
 - 2. *Anafilaroides rostratus* Gerichter, 1949; from Ceylon.

Of the various nematodes in the Filaroididae, *Oslerus osleri* (Figs. 1-4) appears to have certain characters not noticed before. The specimens examined had a protrusible rostrum, consisting of six small equal lips and a peculiar excretory system consisting of three unequal vesicles opening by a common duct very near the anterior end (Fig. 1). In these respects and in the presence of a

common depression into which the vulva and the anus open, the genus *Oslerus* Hall, 1921 resembles the genus *Anafilaroides* Gerichter, 1949. The only difference is that vulvar and vaginal sphincters are absent in *Oslerus*.



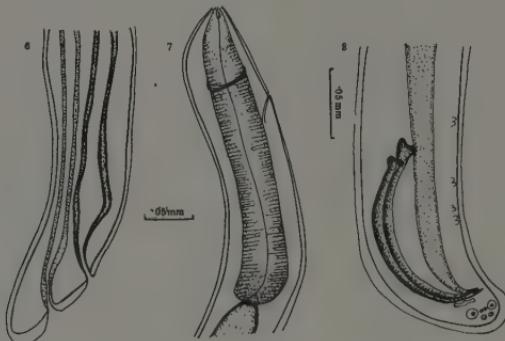
Oslerus osleri (Cobbold, 1879)

Fig. 1.—Anterior end of male, lateral view. Fig. 2.—Posterior end of male, ventral view. Fig. 3.—Posterior end of male, lateral view. Fig. 4.—"En face" view of anterior end. (a) Dorso-lateral papilla. (b) Dorso-dorsal papilla. (c) Interno-dorsal papilla (rudimentary). (d) Amphid. (e) Mouth opening. (f) Lip. (g) Ventro-ventral papilla. (h) Latero-ventral papilla. Fig. 5.—Posterior end of female, lateral view.

Skrjabin (1940) reduced the genus *Oslerus* to a sub-genus of *Filaroides* v. Beneden, 1858. Dougherty (1943b) ignored sub-genera in nematode systematics and considered *Oslerus* a synonym of *Filaroides*. However, the detailed morphology of the anterior end or the nature of the excretory system of *Oslerus* was not then known. Since the work of Chitwood and Wehr (1934), cephalic structures are considered important in nematode classification. Dougherty (1952) has again stressed this point in the further classification of the genus *Metathelazio* Skinker, 1931 in which all members have very uniform characters except in the nature of the cephalic end (Gerichter, 1948).

The genera *Oslerus* and *Anafilaroides* are very uniform but they differ considerably from the genus *Filaroides* (Figs. 6–8), in (1), the nature of the excretory system; (2) the nature of the anterior

end and (3) the relative positions of the anus and vulva. Therefore the genus *Oslerus* is restored and the subfamily Oslerinae Khera, 1956 is recognised to accommodate *Oslerus* and *Anafilaroides*. The definition of the subfamily and a list of the genera and their species are given at the end of this paper.



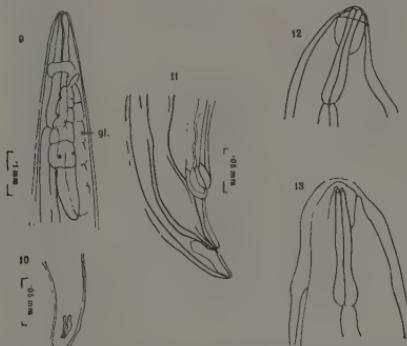
Filaroides martis (Werner, 1782)

Fig. 6.—Posterior end of female, lateral view. Fig. 7.—Anterior end of female, lateral view. Fig. 8.—Posterior end of male, ventro-lateral view.

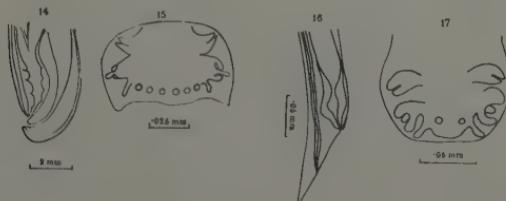
The genus *Parafilaroides* Dougherty, 1946 (Figs. 9–13) shows some resemblances to *Oslerus* and *Anafilaroides*. All genera have rather short spicules, lack a bursa and have the anus and the vulva very close to each other and to the posterior end. All are degenerate genera and *Parafilaroides* is the most degenerate genus in the Filaroididae; it probably represents the end product of an evolutionary process. The habitat of this genus in the lungs of the Pinnipedia, the relative position of the vulva and the anus, and the nature of the anterior end would indicate a close relationship of this genus to the other lungworms of the family Pseudaliidae Railliet, 1916.

Though it was possible to examine *P. decorus*, it was difficult to study in detail the anterior end and the details of the excretory system as the worms are very degenerate and fragile and as these structures are well seen in fresh specimens only. These resemblances of *Parafilaroides* to Oslerinae and Pseudaliidae are considered to be of little significance and until more accurate morphological data are known it is not proposed to alter the systematic position given to *Parafilaroides* by Dougherty (1946) and Skrjabin *et al.* (1952).

The two genera, *Marsupostrongylus* Mackerras and Sandars, 1953 (Figs. 14–15) and *Plectostrongylus* Mackerras and Sandars, 1953 (Figs. 16–17) show a reduced bursa and one or more pairs of rudimentary dorsal rays, and therefore the subfamily *Marsupostrongylinae subfam. nov.* is erected to accommodate them. The definition of this subfamily and the genera and the species in it are given at the end of this paper.



Parafilaroides Dougherty, 1946. (All figures after Dougherty and Herman, 1947) Fig. 9.—Anterior end of female *Parafilaroides decorus*, Dougherty and Herman, 1947, lateral view. Note the sub-ventral glands (Gl.). Fig. 10.—Posterior end of male *P. decorus*, ventro-lateral view. Fig. 11.—Posterior end of female *P. decorus*, lateral view. Fig. 12.—*Parafilaroides prolificus* Dougherty and Herman, 1947, anterior end of female. Note the rostrum like structure. Fig. 13.—*Parafilaroides nanus* Dougherty and Herman, 1947, anterior end of female. Note the lip-like structures at the anterior end.



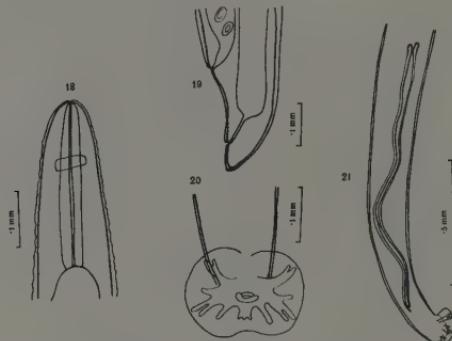
Marsupostrongylus bronchialis Mackerras and Sandars, 1953 after Mackerras and Sandars, 1953

Fig. 14.—Posterior end of female. Fig. 15.—Male bursa.

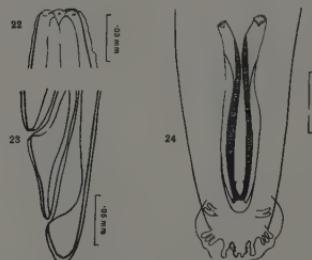
Plectostrongylus fragilis Mackerras and Sandars, 1953, after Mackerras and Sandars, 1953

Fig. 16.—Posterior end of female. Fig. 17.—Male bursa.

Filaroididae appears to include a group of lung-inhabiting nematodes, which possess similar acquired morphological characters though some of them appear to have been evolved from different groups. They have acquired these characters because of their common habitat, the lung. Together with the acquired characters, some ancestral characters are still maintained.



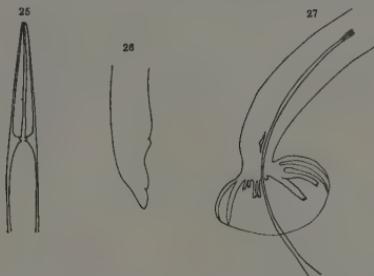
Angiostrongylus cantonensis (Chen, 1935). All figures after Chen, 1935
Fig. 18.—Anterior end. Fig. 19.—Posterior end of female. Fig. 20.—Caudal bursa. Fig. 21.—Tail of male, lateral view.



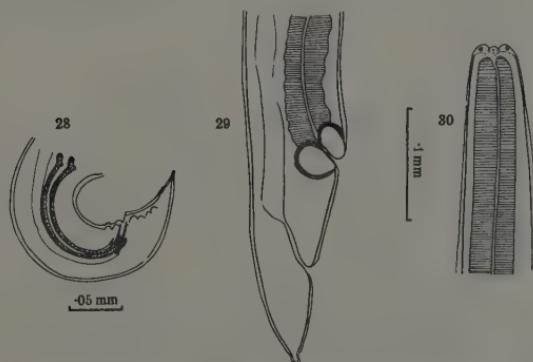
Aelurostrongylus abstrusus (Railliet, 1898)
Fig. 22.—Anterior end, after Gerichter, 1949. Fig. 23.—Posterior end of female, after Cameron, 1927. Fig. 24.—Male bursa, ventral view, after Gerichter, 1949.

The genera *Angiostrongylus* Kamensky, 1905 (Figs. 18–21) and *Aelurostrongylus* Cameron, 1927 (Figs. 22–24) have a reduced bursa. In this character they resemble the two genera in Marsupostrongylinae, but unlike them the reduction is uniform and all the caudal rays are present and are more or less of equal size. The genus

Gurltia Wolffhügel, 1933 (Figs. 25–27) shows a peculiar reduction in the caudal bursa. In this genus all the caudal rays are of unequal size and the dorsals are much smaller than the ventrals and the laterals. The genus *Rodentocaulus* Schulz, Orlov and Kutas, 1933 shows an asymmetrical bursa and stout bursal rays and therefore cannot be considered a synonym of *Angiostrongylus* as stated by Dougherty (1946). As in the previous systems of classification



Gurltia paralysans Wolffhugel, 1933. All figures after Wolffhugel, 1934
Fig. 25.—Anterior end. Fig. 26.—Posterior end female, lateral view. Fig. 27.—
Posterior end of male.

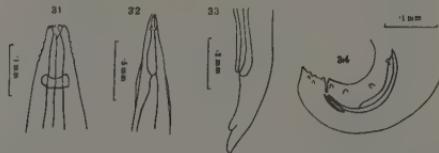


Vogeloides ramanujacharii Alwar, Lalitha and Seneviratna, 1958 from Madras cats
(Original)
Fig. 28.—Posterior end of male. Fig. 29.—Posterior end of female. Fig. 30.—
Anterior end of male.

these four genera are placed in the *Angiostrongylinae* Böhm and Gebauer, 1934. There is little doubt that members of this subfamily are closely related to the *Metastrongylinae* and that both these subfamilies had common ancestors.

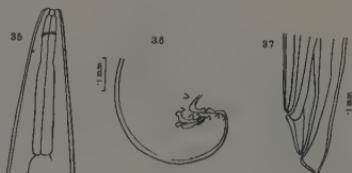
The systematic position of the *Vogeloidinae* Dougherty, 1951

has been problematical. This subfamily consisting of three genera *Vogeloides* Dougherty, 1952 (Figs. 28-30), *Metathelazia* Skinker, 1931 (Figs. 31-34), and *Pneumospirura* Wu and Hu, 1938 (Figs. 35-37), was placed by Dougherty (1952) in the Metastrongylidae. However, Skinker (1931) placed *Metathelazia* in the Thelaziidae and Wu and Hu (1938) placed *Pneumospirura* in their family Pneumospiruridae, in the superfamily Spiruroidea. *Pneumospirura* has such close similarity to the spirurids that one finds it extremely difficult to reach a satisfactory conclusion regarding its systematic position. Chabaud (1949) placed *Metathelazia* only, in the Metastrongylidae and he (1954) later placed *Vogeloides* and *Pneumospirura* in the Spiruroidea. Despite the variation in the cephalic



Metathelazia californica Skinker, 1931, after Skinker, 1931

Fig. 31.—Anterior end, dorsal view. Fig. 32.—Anterior end, lateral view. Fig. 33.—Tail of female, lateral view. Fig. 34.—Tail of male, lateral view.



Pneumospirura hainanensis Wu and Hu, 1938, after Wu and Hu, 1938

Fig. 35.—Anterior end, dorso-ventral view. Fig. 36.—Posterior end of male, lateral view. Fig. 37.—Posterior end of female, lateral view.

characters, such marked separation of the genera is not justifiable because other features, such as the relative shape of the oesophagus, the spicules, the ova and the position of the vulva and the anus, are the same. According to the present state of our knowledge, it is expedient to leave these three genera in the Filaroididae. It is probable that the species of *Pneumospirura* are closely related to the spirurids, and that the Vogeloidinae had a common ancestor with the spirurids, *Pneumospirura* being the closest and *Metathelazia* the farthest relatives, of the spirurids.

At variance with these observations, there are in *Pneumospirura* certain similarities to the lungworms of the Cetacea. The buccal capsule of *Pneumospirura* resembles closely that of the genus *Stenurus* Duj., 1894, a genus which has a well developed buccal capsule (Baylis and Daubney, 1926). In the relative position of the vulva and the anus too, *Pneumospirura* resembles the lungworms of the Cetacea. This evidence is considered sufficient to place the Vogeloidinae in the Metastrogyloidea.

Without knowledge of the life history of any member of the Vogeloidinae it is difficult to state its systematic position with accuracy. If the life history involved an arthropod they should be transferred to the family Pneumospiruridae Wu and Hu, 1933 and placed in the Spiruroidea. The separation of the three genera of the Vogeloidinae and their inclusion in two superfamilies as suggested by Chabaud (1949 and 1954), seems to be quite unjustifiable.

In any system of nematode classification difficulty arises when two individuals of separate genera do not differ markedly from each other even though the genera themselves may be sharply defined. Thus, *Oslerus osleri*, the genotype of *Oslerus* Hall, 1921 is distinct and shows marked dissimilarities from *Filaroides martis*, the genotype of *Filaroides* v. Beneden, though *F. gordius* and *F. barretoi* show some of the characteristics of *Oslerus*. This tendency to depart from the genotype and to resemble another genus is true of all organisms living in a common environment, because they constantly but slowly undergo evolutionary changes, and under these circumstances, they tend to exhibit evolutionary convergence. In no system of classification would all species of one genus be sharply demarcated from all the species of a closely related genus.

From the above observations it appears that the family Filaroididae consists of heterogeneous members that have probably arisen from different ancestors, possessing similar characters as a result of evolutionary convergence, because of their common habitat, the lungs of mammals. Due to their different origins they possess a greater diversity of character than is found in any other nematode family of similar size. The genera that had probably a common origin are placed in the respective subfamilies, and it is likely that as our knowledge increases some of them will have to be separated into different families.

The family Filaroididae is now defined. This is followed by a key to its subfamilies and genera, and a list of the species in the Filaroididae.

FILAROIDIDAE Schulz, 1951

Diagnosis: Metastrongyloidea, Lane, 1917. Found in the lungs or blood vessels of carnivores, rodents, primates or sea-lions. The worms are slender, fragile, small or of moderate length. The tegumental sheath is wide. The caudal bursa and the bursal rays are absent or reduced. Female much larger than the male, with vulva near the posterior end and close to the anus. Oral papillary pattern variable but the internal circle of six papillae seen to be present wherever the "en face" view has been studied; oesophagus usually single but sometimes double; female prodelphic; gubernaculum if present is simple. The anterior end in some cases may be provided with a rostrum. Three or six inconspicuous or small lips generally present.

KEY TO THE SUBFAMILIES AND GENERA IN THE FILAROIDIDAE

- A. Caudal bursa absent (B)
 - 1. Oesophagus single. (2)
 - (a) Anterior end with protrusible rostrum : *Oslerinae* Khera, 1956.
 - (i) Vaginal and vulvar sphincters absent : *Oslerus* Hall, 1921.
 - (ii) Vaginal and vulvar sphincters present :
Anafilaroides Gerichter, 1949.
 - (b) Anterior end without protrusible rostrum : Filaroidinae Skrjabin, 1933.
 - (i) Spicules arcuate and more than 50 microns long ; parasites of terrestrial mammals : *Filaroides* v. Beneden, 1858.
 - (ii) Worms degenerate, spicules less than 50 microns long ; parasites of sea lions : *Parafilaroides* Dougherty, 1946.
 - 2. Oesophagus double : Vogeloidinae Dougherty, 1951.
 - (a) Lips present : *Vogeloides* Dougherty, 1952

(b) Lips absent, buccal capsule insignificant :
Metathelazia Skinker, 1931.

(c) Lips absent, buccal capsule present and well chitinised :
Pneumospirura Wu and Hu, 1938.

B. Caudal bursa present but reduced.

1. All caudal rays present ; Angiostrongylinae Böhm and Gebauer, 1934.

(a) All caudal rays more or less of equal size.

(i) Spicules long, slender and simple, gubernaculum absent except in *A. gubernaculatus* : *Angiostrongylus* Kamensky, 1905.

(ii) Spicules sheathed or alate and of moderate length, gubernaculum present : *Aelurostrongylus* Cameron, 1927.

(b) The dorsal rays are extremely small when compared with the well developed ventral and laterals.

(i) Spicules long, slender and simple, gubernaculum present : *Gurltia* Wolfhügel, 1934.

(c) Caudal bursa asymmetrical, bursal rays stout.

(i) Spicules alate, gubernaculum present : *Rodentocaulus* Schulz, Orlov and Kutas, 1933.

(2) Some caudal rays rudimentary : Marsupostrongylinae *subfam. nov.*

(a) Dorso-dorsal rays rudimentary, gubernaculum absent : *Marsupostrongylus* Mackerras and Sandars, 1953.

(b) Dorso-dorsal and latero-dorsal rays rudimentary, gubernaculum present : *Plectostrongylus* Mackerras and Sandars, 1953.

LIST OF SPECIES IN FILAROIDIDAE:

- Subfamily I : *FILAROIDINAE* Skrjabin, 1933.
- Type genus : *Filaroides* v. Beneden, 1858.
- Synonymy : *Filariopsis* v. Thiel, 1926 ; *Pseudostrongylus* Cameron, 1927.
- Genotype : *F. martis* (Werner, 1782) Dougherty, 1943.
- Synonymy : *Gordius martis* Werner, 1782 ; *Filaria mustelarum pulmonalis* Rudolphi, 1819 ; *Filaroides mustelarum* (Rudolphi, 1819) v. Beneden, 1858.
- Type host : Pine marten, *Martes m. martes* (Linné).
F. barretoi (Travassos, 1921) Gebauer, 1933.
- Synonymy : *Oslerus barretoi* Travassos, 1921.
- Type host : Common squirrel monkey, *Saimiri sciurea* (Linné).
F. gordius (Travassos, 1921) Gebauer, 1933.
- Synonymy : *Oslerus gordius* Travassos, 1921.
- Type host : Common marmoset, *Callithrix jacchus* (Linné).
F. asper (v. Thiel, 1926) Skrjabin, 1940.
- Synonymy : *Filariopsis asper* v. Thiel, 1926.
- Type host : Red howler, *Alouatta seniculus* (Linné).
F. arator (Chandler, 1931) Skrjabin, 1940.
- Synonymy : *Filariopsis arator* Chandler, 1931.
- Type host : *Cebus* sp.
F. cebi Gebauer, 1933.
- Type host : The capuchin monkey, *Cebus macrocephalus* (Linné).
F. myonactis (Sandground, 1937) Dougherty, 1943.
- Synonymy : *Filaroides myonaxi* Sandground, 1937.
- Type host : A black-tipped mongoose, *Myonax sanguineus proteus* (Allen).

F. milksi Whitlock, 1956.

- Type host : Domestic dog, *Canis familiaris* (Linné).
- Subfamily II : *ANGIOSTRONGYLINAE* Böhm and Gebauer, 1934.
- Type genus : ***Angiostrongylus*** Kamensky, 1905.
- Synonymy : *Haemostrongylus* Railliet and Henry, 1907 ; *Parastongylus* Baylis, 1928 ; *Pulmonema* Chen, 1935 ; *Cardionema* Yamaguti, 1941 ; *Rattostrongylus* Schulz, 1951 ; *Angiocaulus* Schulz, 1951.
- Genotype : *A. vasorum* (Baillet, 1866) Kamensky, 1905.
- Synonymy : *Strongylus vasorum* Baillet, 1866 ; *Haemostrongylus vasorum* (Baillet, 1866) Railliet and Henry, 1907.
- Type host : Domestic dog, *Canis familiaris* (Linné).
- A. raillieti* (Travassos, 1927) Dougherty, 1946.
- Synonymy : *Haemostrongylus raillieti* Travassos, 1927.
- Type host : Crab eating dog, *Dusicyon thous azarae* (Wied).
- A. tateronae* (Baylis, 1928) Dougherty, 1946.
- Synonymy : *Parastongylus tateronae* Baylis, 1928.
- Type host : Kemp jerboa, *Tatera kempfi* Wroughton.
- A. cantonensis* (Chen, 1935) Dougherty, 1946.
- Synonymy : *Pulmonema cantonensis*, Chen, 1935 ; *Haemostrongylus ratti* Yokogawa, 1937 ; *Haemostrongylus ratti* Matsumoto, 1937 ; *Rattostrongylus cantonensis* (Chen, 1935) Schulz, 1951.
- Syntype hosts : Norway rat, *Rattus norvegicus* (Erxleben) and common house rat, *Rattus r. rattus* (Linné).
- A. ten* (Yamaguti, 1941) Dougherty, 1946.
- Synonymy : *Cardionema ten* Yamaguti, 1941.
- Type host : Common black-footed marten, *Martes m. melampus*.

A. gubernaculatus Dougherty, 1946.

Synonymy : *Angiocaulus gubernaculatus* (Dougherty, 1946)
Schulz, 1951.

A. soricis Soltys, 1953.

Type host : *Sorex minutus*.

A. blarini Ogren, 1954.

Type host : Short-tailed shrew, *Blarina brevicauda* (Say).

Aelurostrongylus Cameron, 1927.

Synonymy : *Perostrongylus* Schlegel, 1934.

Genotype : *A. abstrusus* (Railliet, 1898) Cameron, 1927.

Synonymy : *Strongylus pusillus* Mueller, 1890 ; *Strongylus abstrusus* Railliet, 1898 ; *Synthetocaulus abstrusus* (Railliet, 1898) Railliet and Henry, 1907.

Type host : Domestic cat, *Felis catus* Linné.

A. brauni (v. Linstow, 1897) Dougherty, 1946.

Synonymy : *Strongylus brauni* v. Linstow, 1897.

Type host : Indian civet, *Viverra zibetha* (Linné).

A. falciformis (Schlegel, 1933) Wetzel, 1938.

Synonymy : *Strongylus falciformis* Schlegel, 1933 ; *Perostrongylus falciformis* (Schlegel, 1933) Schlegel, 1934 ; *Filaroides falciformis* (Schlegel, 1933) Wetzel, 1938.

Type host : Common European badger, *Meles m. meles* (Linné).

Pulmostrongylus Hsu, 1935.

Genotype : *Pulmostrongylus fengi* Hsu, 1935.

Type host : Crab-eating mongoose, *Herpestes urva* Hodgson.

P. herpestis (Khera, 1956) Yeh, 1958.

Synonymy : *Herpestostrongylus herpestis* Khera, 1956.

Host : Mongoose, *Herpestes* sp.

Guritia Wolffhügel, 1933.

Genotype : *G. paralysans* Wolffhügel, 1933.

Syntype hosts : Domestic cat, *Felis catus* Linné and spotted tiger cat, *Felis g. guigna* Molina.

Rodentocaulus Schulz, Orlov and Kutas, 1933.

Genotype : *R. ondatrae* Schulz, Orlov and Kutas, 1933.

Synonymy : *Angiostrongylus ondatrae* (Schulz, Orlov and Kutas, 1933) Dougherty, 1946.

Type host : Muskrat, *Ondatra zibethica* (Linné).

Subfamily III : *MARSUPOSTRONGYLINAE* subfam. nov.

Diagnosis : Filaroididae, caudal bursa present but reduced ; this reduction being most marked in the dorsal rays. The dorso-dorsal, or the dorso-dorsal and dorso-lateral rays represented by papillae. Gubernaculum present or absent. Anterior end with six equal lips. Vulva and anus close to each other or may be in a common depression.

Type genus : **Marsupostrongylus** Mackerras and Sandars, 1953.

Genotype : *M. bronchialis* Mackerras and Sandars, 1953.

Type host : The bandicoot, *Isodon obesula*.

Plectostrongylus Mackerras and Sandars, 1953.

Genotype : *P. fragilis* Mackerras and Sandars, 1953.

Type host : *Antechinus flavipes*.

*Subfamily IV: *OSLERINAE* Khera, 1956, emend. nov.

Diagnosis : Filaroididae, anterior end with protrusible rostrum consisting of six equal lips. Excretory system consisting of three unequal, large vesicles opening by a common duct near the anterior end. Caudal bursa absent and the spicules of moderate length, stout, slightly curved and alate. Post cloacal papillae generally arranged in pairs and variable in number. Anus and vulva situated close together

* See next page for footnote.

in a common depression near the tail end, this depression guarded by three unequal flaps. Uterine and vulvar sphincters absent or present. Viviparous or ovoviviparous. Wherever known development is in molluscs. *Parasites of carnivores.*

- Type genus : ***Oslerus*** Hall, 1921 restored. Uterine and vulval sphincters absent. Parasites of Canidae.
- Genotype : *O. osleri* (Cobbold, 1879) Hall, 1921.
- Synonymy : *Strongylus canis bronchialis* Osler, 1877 ; *Filaria osleri* Cobbold, 1879 ; *Pseudalium osleri* (Cobbold, 1879) Railliet, 1915 ; *Filaroides (Oslerus) osleri* (Cobbold, 1879) Skrjabin, 1933.
- Type host : Domestic dog, *Canis familiaris* Linne.
- O. kreisi* (Dougherty, 1943) comb. nov.
- Synonymy : *Stenurus* sp. Kreis, 1938 ; *Filaroides kreisi* Dougherty, 1943.
- Type host : Cape hunting dog, *Lycaon pictus* (Temminck).

* Professor J. J. C. Buckley of the London School of Hygiene and Tropical Medicine has kindly drawn my attention to two papers that have appeared since the above publication was prepared for press, viz.:

KHERA, S. (1956).—"Nematode parasites of some Indian Vertebrates." *Indian J. Helminth.*, 6 (2), 27-133. (September, 1954.) ; and
 YEH, LIANG-SHENG (1958).—"A redescription of *Pulmostrongylus herpestes* (S. Khera, 1956) n.comb. from the lung of a mongoose, *Herpestes* sp., from Suva, Fiji." *J. Helminth.*, 32, (1/2), 93-98.

In the first paper Khera erects a new sub-family *Osleriinae* with type genus *Oslerus* Hall, 1921 and places it in the Family Dipetalonematidae Wehr, 1935. The sub-family should read *Oslerinae* and not *Osleriinae* (vide International Rules of Nomenclature, Article 4). Yeh has correctly pointed out, that he sees no reason as to why this sub-family should have been placed under Dipetalonematidae Wehr, 1935 of the filarioids. The synonymy of *Oslerus* has been discussed in the present paper and the reasons for its restoration have been stated, whilst in another paper to be published in collaboration with Dr. J. N. Oldham, a full description of *Oslerus osleri* (Cobbold, 1879) is given.

The suppression of *Osleriinae* Khera, has been suggested by Yeh (1958). This subfamily should be retained as the synonymy of *Papilloslerus* should not affect *Oslerus* or *Oslerinae*. The genus *Papiloslerus* resembles *Metathelazia* closely, but it differs from the latter in the lack of division of oesophagus, and the presence of irregularly scattered prominent papillae situated on the body, except at the oesophageal and tail region. However, these characters are not considered to be of significance to warrant the erection of a new genus, particularly when more precise data on the peri-oral structure or caudal end of the male are lacking.

Anafilaroides Gerichter, 1949.

- Genotype : *A. rostratus* Gerichter, 1949.
- Synonymy : *Filaroides rostratus* (Gerichter, 1949) Dougherty, 1951.
- Type host : Domestic cat, *Felis catus* Linné.
- Subfamily V : *VOGELOIDINAE* Dougherty, 1951.
- Type genus : **Vogeloides** Dougherty, 1952.
- Synonymy : *Osleroides* Orlov, Davtian and Lubimov, 1933.
- Genotype : *Vogeloides ascaroides* (v. Linstow, 1879) Dougherty, 1952.
- Synonymy : *Filaria ascaroides* v. Linstow, 1879 *Metathelazia ascaroides* (v. Linstow, 1879) Dougherty, 1943.
- Type host : Mona guenon, *Cercopithecus mona* (Linné).
- Vogeloides zorillae* (Seurat, 1919) Dougherty, 1952.
- Synonymy : *Hartertia zorillae* Seurat, 1919. *Metathelazia zorillae* (Seurat, 1919) Chabaud, 1949.
- Type host : Vaillant's zoril, *Poeciliictis libyca vaillanti* (Loche).
- V. massinoi* (Davtian, 1933) Dougherty, 1952.
- Synonymy : *Osleroides massino* Davtian, 1933. *Metathelazia massino* (Davtian, 1933) Dougherty, 1943. *Metathelazia massinoi* (Davtian, 1933) Dougherty, 1949.
- Type host : Domestic cat, *Felis catus* Linné.
- V. oesophageus* (Gerichter, 1948) emend. nov.
- Synonymy : *Metathelazia oesophagea* Gerichter, 1948 *Vogeloides oesophagea* (Gerichter, 1948) Dougherty, 1952.
- Type host : Mongoose, *Herpestes ichneumon* Linné.
- V. servalis* (Chabaud and Biocca, 1950) Dougherty, 1952.
- Synonymy : *Metathelazia servalis* Chabaud and Biocca, 1950.
- Type host : *Felis serval* Schreber.

V. exilis (Biocca and Chabaud, 1952) *comb. nov.*

Synonymy : *Metathelazia exilis* Biocca and Chabaud, 1952.

Type host : Mongoose, *Herpestes caffer* (Gmelin).

V. ramanujacharii Alwar, Lalitha and Seneviratna, 1958.

Type host : Domestic cat, *Felis catus* Linné.

Metathelazia Skinker, 1931.

Synonymy : *Papilloslerus* Khera, 1956.

Genotype : *Metathelazia californica* Skinker, 1931.

Syntype hosts : Californian Wild Cat, *Felis rufa californica* (Mearns) and Rocky mountain lion, *Felis concolor hippolestes* Merriam.

M. erinaceus (Khera, 1956) Yeh, 1958.

Synonymy : *Papiloslerus erinaceus* Khera, 1956.

Host : Hedgehog, *Erinaceus* sp.

M. felis (Vogel, 1928) Dougherty, 1943.

Synonymy : *Oslerus felis* Vogel, 1928.

Type host : Ocelot or tiger cat, *Felis pardalis* Linné.

M. multipapillata Gerichter, 1948.

Type host : Palestine hedgehog, *Erinaceus roumanicus sacer* Thomas.

Pneumospirura Wu and Hu, 1938.

Genotype : *P. hainanensis* Wu and Hu, 1938.

Synonymy : *Metathelazia hainanensis* (Wu and Hu, 1938) Dougherty, 1943.

Type host : Eastern Chinese otter, *Lutra lutra chinensis* Gray.

P. capsulata (Gerichter, 1948) Dougherty, 1952.

Synonymy : *Metathelazia capsulata* Gerichter, 1948.

Type host : European badger, *Meles meles* Linné.

SUMMARY

The family Filaroididae Schulz, 1951 is defined and reclassified into five subfamilies, viz.: Filaroidinae Skrjabin, 1933; Angiostrongylinae Bohm and Gebauer, 1934; Vogeloidinae Dougherty, 1951; Oslerinae Khera, 1954; and Marsupostrongylinae *subfam. nov.* Definitions of the last two sub-families are given and the familial relationships of the Filaroididae are discussed. All species in the Filaroididae are listed and a key is given to its sub-families and genera.

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On a New Species of *Proteocephalus* from Brazil*

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As the interesting and complex family the Proteocephalidae is represented by several forms not only from the Sudan but from various parts of the world, a brief summary of it is made below.

With the exception of Weinland (1858), investigators up to the time of Monticelli (1891) considered this group of fish cestodes to belong to the genus *Taenia* Linnaeus, 1758. It was Weinland who removed them from this genus, and erected that of *Proteocephalus* for them with *T. ambigua* Dujardin as the type, and *T. filicollis* and *T. dispar* as additional members.

In 1891, Linstow pointed out that the fish species made a closely related group on account of certain constantly occurring characters. His observations were based on the structure and development of *Taenia longicollis* Rudolphi. In the same year Monticelli also made a careful study of the group, his work being largely based upon *Taenia coryphicephala* with which he compared other species. The result of this work was the separation of about twenty forms for which he erected the genus *Tetracotylus*.

Loennberg (1894) erected the genus *Ichthyotaenia* to accommodate Rudolphi's *T. ocellata* and *T. filicollis*, and Ariola (1899) placed the genus in a special family which he called the Ichthyotaenidae.

In 1911 La Rue created the family Proteocephalidae to include the genera *Proteocephalus* Weinland, 1858, *Corallobothrium* Fritsch, 1886, *Crepidobothrium* Monticelli 1899, *Acanthotaenia* Linstow, 1903, *Choanoscolex* La Rue, 1911, and *Ophiotaenia* La Rue, 1911. He discussed the homonymy of Monticelli's (1891) *Tetracotylus* and Filippi's (1854) *Tetricotyle*, and proposed the name *Monticellia* for the former. He was not able to admit the genus to his family, the Proteocephalidae, because of striking differences in the internal arrangement of the genitalia, and accordingly created a separate family for it, the Monticelliidae.

* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

By this time (1914) there was considerable confusion in the classification of this group of tapeworms, but it was substantially reduced by the publication of La Rue's "Revision of the Cestode Family Proteocephalidae." In this work he proposed the retention of Weinland's *Proteocephalus*, with the consequent suppression of Loennberg's *Ichthyotaenia* on the grounds that Loennberg's type species is synonymous with Weinland's. This view was almost unanimously accepted, and the proteocephalan tapeworms were subdivided into two families: the Proteocephalidae with six genera (previously enumerated), and the Monticelliidae with a single genus, *Monticellia* La Rue, 1911.

This scheme persisted until 1925 with comparatively few changes, except for the addition of a few new genera. In this year Southwell placed the Proteocephalidae with the Lecanicephalidae in a sub-order, the Multivittellata, of the order Cyclophyllidea, and added *Marsypocephalus rectangularis* Wedl, 1861 to the Proteocephalidae. Fuhrmann and Baer redefined the Monticelliidae and added to it the genera *Loennbergia* Fuhrmann and Baer, *Ephedocephalus* Diesing, and *Goezeella* Fuhrmann. The genus *Rudolphiella* fell into synonymy with *Ephedocephalus*.

Meggitt (1927) surveyed La Rue's scheme and retained the family Monticelliidae, but persisted in his refusal (1914) to accept the Proteocephalidae and revived the family Ichthyotaeniidae, and the genus *Ichthyotaenia*. In the family Monticelliidae he placed the genera *Ephedocephalus*, *Goezeella*, *Loennbergia*, *Marsypocephalus* and *Monticellia*; in the Ichthyotaeniidae he placed the genera *Corallobothrium*, *Crepidobothrium*, *Gangesia* and *Ichthyotaenia*. For the very large number of species of *Crepidobothrium* and *Ichthyotaenia* (58 species each) he created species groups as a means of division, and used various structural features for distinguishing species-groups, and component species within each group. This has been said to be a workable though somewhat artificial method of separating the proteocephalan species.

Woodland worked on a mass of material from African and South American siluroid fishes, and surveyed the known proteocephalan worms in a series of publications from 1925-37, and in 1925 suggested their inclusion in a single family, the Proteocephalidae, with a much reduced number of genera. The majority of proteocephalan forms were placed in a sub-family, the Proteocephalinae with the type genus *Proteocephalus* into which he incorporated such genera

as *Ophiotaenia*, *Ophidiotaenia*, *Acanthotaenia*, *Solenotaenia*, *Gangesia*, *Corallobothrium*, *Batrachotaenia*, and *Choanoscolex*. This scheme was the outcome of his view that scolex characters are of no value for defining genera. Since Woodland's scheme calls for the inclusion of the large majority of proteocephalans within the one genus, *Proteocephalus*, it aggravates the difficulty of subdividing the unwieldy mass of species. Woodland himself found it impossible to establish sub-genera within the genus *Proteocephalus*, though he recognized that the proteocephalans from freshwater fishes formed a homogeneous group and suggested the name *Teleostotaenia* for it. For a second large homogeneous group occurring typically in snakes, but also including forms from amphibians, chelonians, and siluroid fishes, he proposed the term *Crepidobothrium*.

Fuhrmann (1931) and Harwood (1933) followed Woodland's scheme, but recognized the genera *Proteocephalus*, *Ophiotaenia*, *Acanthotaenia*, *Crepidobothrium*, *Corallobothrium*, *Gangesia* and *Lintoniella*.

Wardle and McLeod (1952) also adopt Woodland's scheme and recognise the family Proteocephalidae with eight sub-families, but in view of the fact that Woodland's views on the validity of the scolex characters is not generally accepted, they follow, as regards the sub-family Proteocephalinae, the genera recognised by Fuhrmann (1931). Within the genera *Proteocephalus* and *Ophiotaenia* they adopt Meggitt's concept of species-groups.

PROTEOCEPHALIDAE La Rue amend. Woodland, 1933

PROTEOCEPHALUS PLATYSTOMI n.sp.

The material for this species, collected in 1937 from the Amazon siluroid *Platystoma* sp., was deposited unidentified by the late Dr. W. N. F. Woodland in the Helminthology Department, British Museum (Natural History) whence it was very kindly loaned to the writer by Mr. Prudhoe, keeper of Helminths, British Museum (Natural History).

The material consists of a single fragmented specimen thought by Woodland to measure 45 mm., from which he removed three pieces for sectioning. As the specimen stands, the sum of the scolex and fragments is 25 mm.; the strobila is slender and the lateral

margins are smooth, without any notches to demarcate the segments which are distinguished by the repetition of the genitalia. An examination of the strobila shows that the segments mature and become gravid very rapidly. A mature segment measures 1·21 mm. broad by 0·5 mm. long, the segments being broader than long. The genital pore is at about the middle of the lateral margin of the segment.

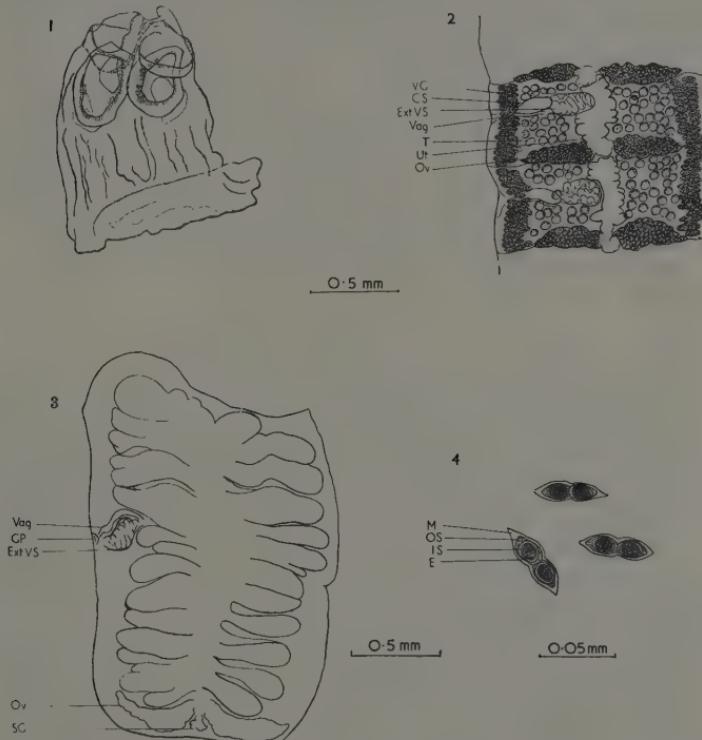
The scolex (Fig. 1) is somewhat distorted; it is 1·25 mm. long by 0·87 mm. broad, and has its entire surface thrown into a series of longitudinal grooves and folds. It bears four large, deep suckers having an irregular shape, and measuring 420–480 μ long by 310–320 μ broad. An apical sucker is absent. There does not appear to be any neck, as all the fragments consist of mature or gravid segments.

The structure of the segment appears to be of the normal proteocephaline type, except that the longitudinal muscle layer appears to be very thin, but nevertheless it contains all the organs. The excretory system apparently consists only of a pair of ventral longitudinal vessels, since no others can be distinguished in the transverse sections.

The testes number 35–50 in each segment, and do not show a strict two-field division, some of them extending in front of the uterine stem wherever space permits. The vas deferens is enormously coiled to form a large external vesicula seminalis which forms an indentation on the side of the uterus. In gravid segments, however, the uterine branches push it towards the lateral margin where remnants of it may be seen. The cirrus sac measures 290–310 μ long by 90–100 μ broad, and may be anterior or posterior to the vagina.

The ovary is situated at the extreme posterior border of the segment, and consists of two very distinct lateral lobes extending on each side to the vitellaria, and united by a median isthmus behind which is an inconspicuous shell gland. The vagina is not readily seen and its position is difficult to determine as it is obscured by the vitellaria, but, as far as can be distinguished, it appears to open posterior to the cirrus sac in some segments (Fig. 2) and anterior to it in others (Fig. 3). The uterus when filled with eggs occupies the entire segment and gives off 12 or 13 diverticula on each side. The gravid segments tend to be longer than broad. The eggs are of a very unusual type (Fig. 4), always occurring in pairs, each pair being contained in an outer shell or membrane which is drawn out to a point at the ends, and is constricted in the middle where the two eggs are in contact with each other. The length of this containing membrane is 50–60 μ . Each egg has two shells, the outer one being

granular and measuring 20–23 μ long by 13–15 μ broad. The inner shell is rather closely applied to the embryo and is hyaline in appearance. The embryo measures 10–12 μ and is devoid of hooks, a condition which is usual in Amazon fish cestodes (Woodland, 1934).



Proteocephalus platystomi n.sp.

Fig. 1.—Scolex. Fig. 2.—Mature segment: VG=vitelline glands; CS=cirrus sac; Ext. VS=external vesicula seminalis; Vag=vagina; T=testes; Ut=uterus; Ov=ovary. Fig. 3.—Gravid segment (outline drawing): Vag=vagina; GP=genital pore; Ext. VS=external vesicula seminalis; OV=ovary; SG=shell gland. Fig. 4.—Eggs: M=membrane; OS=outer shell; IS=inner shell; E=embryo.

This worm closely resembles *Proteocephalus jandia* Woodland, 1924 occurring also in an Amazon siluroid, *Rhamdia* sp. Both worms possess a very much coiled vas deferens which forms an external vesicula seminalis and an ovary consisting of very distinct lateral

lobes united by a median isthmus. The differences between the two worms lie in the size of the scolex and suckers which are smaller in *Proteocephalus jandia* than in the writer's worm; the possession of a long slender unsegmented neck in the former, and its probable absence in the latter; the larger number of testes in the former (under 100) while those of the latter do not exceed 50; the smaller size of the cirrus sac in the former and the presumably constant position of the vagina anterior to it, while in the latter its position is variable.

A final point of difference which separates the writer's worm from *Proteocephalus jandia* and other species of *Proteocephalus* is the unique pairing of the eggs. For these reasons this worm cannot be identified with any of the known species of *Proteocephalus* and is then designated as a new species. *Proteocephalus platystomi*.

The type slide has been deposited in the British Museum (Natural History).

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On a New Species of the Genus *Ganeo* Klein, 1905 and Some Notes on the Genus*

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A single specimen of *Ganeo* was collected from the intestine of *Bufo viridis* in Harwan, Kashmir. It was found to have morphological characters which distinguish it from known species of *Ganeo* and is herein described as a new species.

LECITHODENDRIIDAE Odhner, 1911

PLEUROGENETINAE Looss, 1899

Ganeo Klein, 1905

Ganeo bufonis n.sp.

The body is ovoidal, tapering somewhat towards the anterior end with a broadly rounded posterior end. It measures 1.7 mm. in length and 0.84 mm. in the maximum breadth in the region of the vitellaria. The body surface is covered with backwardly directed minute spines, numerous in the anterior half of the body.

The oral sucker is oval, transversely placed and sub-terminal, measuring 0.114×0.129 mm. The acetabulum is almost equal in size to the oral sucker, measuring 0.12×0.129 mm. It is pre-equatorial, placed 0.69 mm. from the anterior end.

The genital aperture is on the left, midway between the pharynx and the intestinal fork. The genital atrium is 0.12 mm. deep and runs obliquely upward from the genital aperture. The excretory pore is sub-terminal and ventral, 0.05 mm. from the posterior end. The excretory bladder is U-shaped, the median stem being absent.

The mouth leads into a short pre-pharynx 0.04 mm. long. The pharynx is more or less globular, 0.075×0.06 mm. in size. The oesophagus is a long slender tube, 0.25 mm. in length. The intestinal

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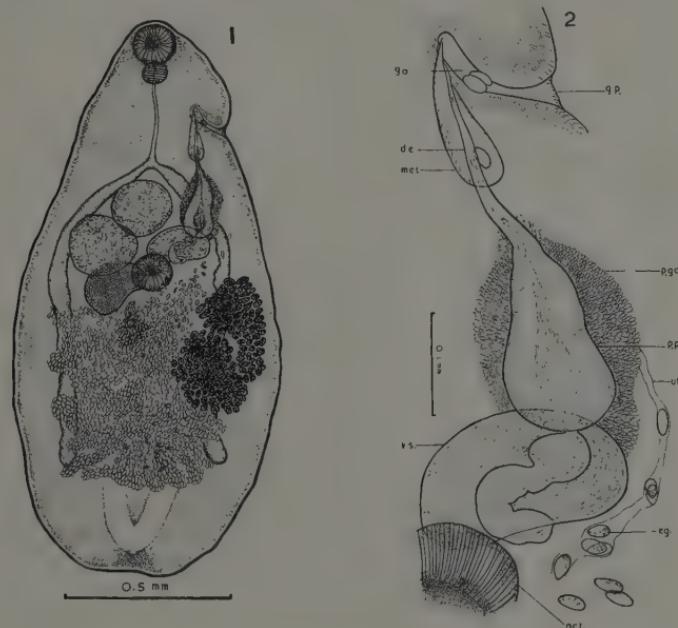
bifurcation is $0\cdot42$ mm. from the anterior end. The caeca terminate $0\cdot3$ mm. from the posterior end. They are well developed and their inner margins are somewhat crenated.

The gonads are close to and partly overlap each other. The testes are smooth and obliquely placed. The anterior testis is median, close behind the intestinal fork and measures $0\cdot195 \times 0\cdot18$ mm. The posterior testis is on the right side of the acetabulum extending to its middle level, and measures $0\cdot24 \times 0\cdot195$ mm. It is larger than the anterior testis and partly overlaps it. Both the testes are close to the right intestinal caecum and partly overlap it ventrally. There is no cirrus sac nor pseudo cirrus sac. The seminal vesicle is a thin-walled oval structure, transversely placed on the left side between the left intestinal caecum and the testes. It partly overlaps the acetabulum dorsally. A narrow curved distal tube arises from its posterior border and opens into the pars prostatica. The main body of the seminal vesicle measures $0\cdot2 \times 0\cdot11$ mm. The pars prostatica is a well developed elongated tube, broad and rounded at the base and gradually narrowing anteriorly. It measures $0\cdot25 \times 0\cdot09$ mm. Numerous diffused prostatic gland cells lie freely in the surrounding parenchyma. The ejaculatory duct is a long narrow tube, running ventrally to the metraterm before opening into the genital atrium.

The ovary is bean-shaped and is placed slightly obliquely to the right side of the acetabulum which is partly overlapped by it dorsally. Most of the ovary is behind the posterior border of the acetabulum. It is smaller than the posterior testis, measuring $0\cdot21 \times 0\cdot165$ mm. The seminal receptacle lies immediately behind, on the left side of the ovary and posterior to the acetabulum. It is pear-shaped, measuring $0\cdot06 \times 0\cdot045$ mm. The uterus is well developed but the convolutions extend hardly $0\cdot06$ mm. beyond the blind ends of the caeca. The uterine coils are compactly filled with numerous eggs and the usual transverse arrangement of the coils is not clearly marked. The caeca are partly overlapped ventrally by the coils. The ascending limb of the uterus runs obliquely on the left side of the seminal vesicle, ventrally over the left intestinal caecum and on the left side of the pars prostatica. It bends at about the middle of the pars prostatica and opens into a well developed and muscular metraterm at the level of the beginning of the ejaculatory duct. The metraterm is shaped like an elongated pear. It measures $0\cdot15 \times 0\cdot045$ mm. Both the vitellaria are placed on the left side, ventral and lateral to the left intestinal caecum. They extend from the level of the acetabulum posteriorly to $0\cdot17$ mm. from the blind end of the left caecum. The eggs are oval and measure $27\text{--}30 \times 12\text{--}15\mu$ in size.

RELATIONSHIPS

The most outstanding feature of this form is the presence of both the vitelline glands on one side, in which it differs from all the known species of the genus *Ganeo*. This feature, however, is not uncommon among the species of the subfamily Pleurogenetinae in which *Ganeo* is also a member. *Pleurogenoides sphaericus* Klein, 1905, *P. taylori* Tubangui, 1928, *Prostotocus himalayi* Pande, 1937



Ganeo bufonis sp.nov.

Fig. 1.—Ventral view. Fig. 2.—Genitalia, enlarged.

act.=acetabulum; d.e.=ductus ejaculatorius; eg.=egg; g.a.=genital atrium; g.p.=genital pore; met.=metraterm; p.g.c.=prostatic gland cells; p.p.=pars prostatica; ut.=uterus; v.s.=vesicula seminalis.

P. kashabia Kaw, 1943 and *P. partapus* Kaw, 1950 have all got one-sided distribution of the vitelline follicles. Kaw (1950) described a young form of *Ganeo*, without eggs in the uterus, which has both the vitellaria confined to the right side. These examples of one-sided vitellaria suggest that this feature is a specific character and not an abnormality.

In all other species of *Ganeo*, the uterine coils extend to the post-caecal area, reaching almost to the posterior end of the body, but in the present specimen they are mostly confined to the intra-caecal space. The excretory bladder is U-shaped without any median stem, and the excretory pore is sub-terminal, opening a short distance anterior to the posterior extremity. The metraterm is muscular and very well developed. The two suckers are more or less of the same size.

The present form resembles *Ganeo glottooides* Klein, 1905 in the topography of the gonads, but differs from it and its sub-species, now raised to the rank of species viz., *G. africana* Skrjabin, 1916 and from *G. madrasensis* Mehra and Negi, 1928 in having no pseudo cirrus sac. It further differs from these species in having a sub-terminal excretory pore and a well developed metraterm. Moreover, it differs from *G. africana* and *G. madrasensis* in the extent of the intestinal caeca and the topography of the gonads. It differs from *G. tigrinum* Mehra and Negi, 1928, *G. attenuatum* Srivastava, 1933, *G. kumaonensis* Pande, 1937 (synonym of *G. tigrinum*), *G. srinagarensis* Kaw, 1950 and *G. panjabensis* Gupta, 1954 in the posterior extent of the uterus and in having no median stem in the excretory bladder. It further differs from *G. gastricus* Srivastava, 1933 and *G. panjabensis* in having a well developed metraterm, and from *G. korkei* Bhalerao, 1936 and *G. gastricus* in the position of the oral sucker. The presence of the spines all over the body of *G. korkei* and an attenuated shape of *G. attenuatum* are yet further differences from the present form. It also differs from *G. gastricus*, *G. korkei* and *G. srinagarensis* in the topography of the gonads. Lastly, it differs from all the known species of the genus in the distribution of the vitelline follicles as discussed in the beginning. Considering these differences, the present form is believed to be a new species to which the name *Ganeo bufonis* is given. This is first species of the genus recorded from a toad.

Host : *Bufo viridis*.

Habitat : Intestine.

Locality : Harwan, Kashmir.

Type : To be deposited in the Dept. of Parasitology, London School of Hygiene and Tropical Medicine.

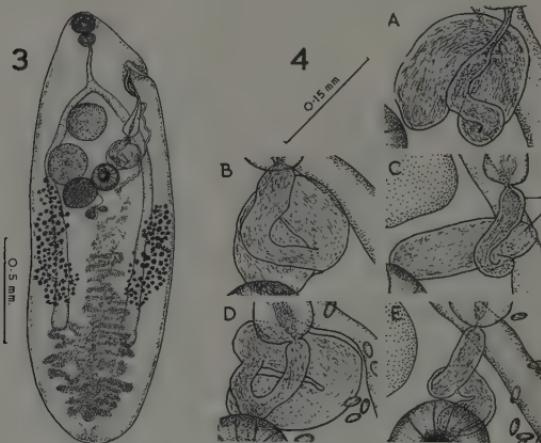
GANEOTIGRINUM Mehra and Negi, 1928
and its identity with *G. kumaonensis* Pande, 1937 and with
G. lingnanensis Li, 1938.

In a subsequent collection of helminth parasites of *Bufo viridis* from Kashmir, the writer found a large number of *Ganeo tigrinum* Mehra and Negi, 1928, which is a new record for this host (Fig. 3). Detailed study of this parasite and its comparison with the figures of *G. kumaonensis* Pande, 1937 and *G. lingnanensis* Li, 1938 show that all three are one and the same species.

Pande (1937) differentiates his species, *G. kumaonensis* from *G. tigrinum* on the basis of the more anterior position of the ovary in relation to the acetabulum; the different shape of the seminal vesicle; small size of eggs; more anterior extent of vitellaria and the presence of a metraterm. The differences in the position of ovary and vitellaria are so slight and inconspicuous that they cannot be accepted as having any specific importance. The ovary in *G. kumaonensis* is slightly anterior but that does not alter its basic position in relation to the acetabulum when compared to that of *G. tigrinum*. Li (1938) also points out a similar sort of difference in *G. lingnanensis*, as having a slightly posterior position of its anterior testis with respect to the intestinal fork. Similar variations were noted by the writer in his collection of *G. tigrinum*. The ovary, which in Fig. 3 is shown to touch the posterior testis and the acetabulum, was found placed in another specimen a short distance posteriorly so as to assume a distinctly post-acetabular position. Similarly, the anterior testis which is usually placed immediately behind the intestinal bifurcation, may take a slightly posterior position. Hence these slight variations in the position of the gonads bear no specific importance.

The vitellaria extend posterior to the middle of the post-acetabular region in both *G. tigrinum* and *G. kumaonensis*, but anteriorly they are said to extend to the posterior border of the acetabulum in the latter, and to the posterior border of the ovary in the former. Since the ovary and the acetabulum are very close to each other, the difference in the anterior extent of the vitellaria is negligible. Variations of similar nature are present in the present specimens of *G. tigrinum*. In Fig. 3, for example, the vitellaria on the right side extend more anteriorly than on the left; thus both the positions mentioned above may occur in the same specimen.

Mehra and Negi (1928) stated that the shape of the seminal vesicle in *G. tigrinum* was variable, depending on the contents and conditions of preservation. The shape of the seminal vesicle in *G. kumaonensis*, stated by Pande to be different, is basically similar to that in *G. tigrinum*. An additional twist in the main body of the organ is a variation of no importance, as illustrated by the presence of several similar variations in the shape of the seminal vesicle in the present specimens of *G. tigrinum* (Fig. 4, a-e). The



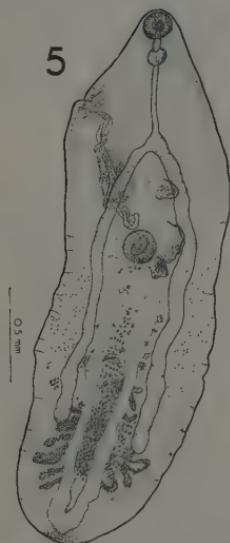
Ganeo tigrinum Mehra and Negi, 1928

Fig. 3.—Ventral view. Fig. 4 (a—e)—Variations in the shape of seminal vesicle.

seminal vesicle is invariably twisted in the species of *Ganeo*. It consists of the main body and a distal tubular part which in turn opens into the pars prostatica. The twisting of the organ brings about apparently different shapes, even among the specimens of the same species, and hence bears no specific importance.

The presence of a metraterm in *G. kumaonensis* and *G. lingnanensis* is also included as one of the differences with *G. tigrinum*. The metraterm, of which Mehra and Negi (1928) made no reference, is recorded in the present specimens of *G. tigrinum*. Hence this difference is also ruled out.

As regards the egg size, which Pande points out to be smaller in his species, it is actually due to the position of the decimal point being misplaced in the egg size of *G. tigrinum*: instead of 0·03 mm. it has been misprinted as 0·3 mm. Li (1938) also records this mistake. The corrected size of the eggs in *G. tigrinum* does not indicate any wide difference. Besides both the sizes are recorded in the present specimens of *G. tigrinum*.



Ganeo sp. (tigrinum ?)

Fig. 5.—Dorsal view.

Li (1938), while stating that his species, *G. lingnanensis*, is closely allied to *G. tigrinum*, separates it on the basis of the presence of a metraterm, the slightly posterior position of the anterior testis and the pestle-shaped pars prostatica. Of these so-called differences the first two have been dealt with above. With regard to the third, from the drawing of *G. lingnanensis* there appears to be no difference whatsoever in the shape of the pars prostatica from that of *G. tigrinum*. In both it is rounded at the base and gradually narrows anteriorly. Even the measurements are the same.

On the basis of the above observations it is considered that *G. kumaonensis* and *G. lingnanensis* are synonyms of *G. tigrinum*.

Ganeo sp. (*tigrinum?*)

A single specimen of *Ganeo* was recovered from the intestine of *Bufo viridis* (Fig. 5). The parasite is related to *G. tigrinum* from which it differs in the absence of the metraterm and median stem in the excretory bladder, presence of a well developed pre-pharynx, and in the shape of the gonads, seminal vesicle and the general body outline. The irregular shape of the gonads with partly diffused contents, the diffused vitelline follicles and the general appearance of the specimen indicate that it is an aged one. For this reason it is rather difficult to identify it with certainty, but it is probably *G. tigrinum*.

REVISED DIAGNOSIS OF THE GENUS *GANEKO* KLEIN, 1905

Body elliptical, oval or tongue-shaped, rarely attenuated; cuticle partly covered with small spines; oral sucker sub-terminal, rarely terminal; acetabulum placed at the margin of anterior third or in the middle third of body; oesophagus short or moderately long; caeca equal or unequal, extending about or beyond three-fifths of body length but never touching posterior extremity; genital pore placed near anterior left body margin, at the level of middle of oesophagus or slightly posterior to it; genital atrium well developed; testes pre- or post-acetabular, oblique or lateral; seminal vesicle usually twisted, pre-acetabular or acetabular; pars prostatica and surrounding prostatic gland cells well developed; cirrus sac absent, pseudo cirrus sac present or absent; ovary pre- or post-acetabular, post-testicular, rarely median; vitellaria lateral and caecal, extent variable, usually terminate in front of blind ends of caeca, may be confined to one side; uterine coils transversely arranged behind acetabulum in intracaecal and post-caecal zone; metraterm present or absent; eggs oval or elliptical, $16-34 \times 9-18\mu$; excretory pore terminal or sub-terminal; excretory bladder U- or V-shaped, with or without median stem.

Habitat and host: Intestine (rarely stomach) of amphibians and fishes.

Distribution: India, China and Africa.

REVISED KEY TO THE SPECIES OF THE GENUS *GANE* KLEIN, 1905

- Pseudo cirrus sac present (A)
 Pseudo cirrus sac absent (B)
- (A) 1. Intestinal caeca do not reach posterior end, testes pre-acetabular, ovary partly behind acetabulum *G. GLOTOOIDES*
 2. Both caeca reach posterior end, ovary and posterior testis post-acetabular ... *G. AFRICANA*
 3. Only right caecum reaches posterior end, all gonads post-acetabular ... *G. MADRASENSIS*
- (B) 1. Vitellaria confined to one side *G. BUFONIS*
 2. Vitellaria on both sides terminate at the level of blind ends of caeca ... *G. PANJABENSIS*
 3. Vitelline follicles arranged in groups of 7 and 5 on right and left side respectively, oral sucker terminal, ovary larger than testes ... *G. KORKEI*
 4. Vitellaria on both sides terminate in front of blind ends of caeca (C)
- (C) 1. Testes lateral and pre-acetabular, oral sucker terminal, ovary on right side of acetabulum *G. GASTRICUS*
 2. Testes lateral and post-acetabular, ovary median, oral sucker sub-terminal ... *G. SRINAGARENSIS*
 3. Testes obliquely placed and pre-acetabular, anterior testis behind intestinal fork, ovary behind posterior testis and smaller than testes, excretory bladder with a short median stem *G. TIGRINUM*
 Syns. *G. kumaonensis*
G. lingnanensis
4. Closely opposed gonads, testes obliquely placed, uterine coils not compact, excretory bladder V-shaped, without median stem, cornua crenated *G. GOBINDIA*
 5. Testes slightly oblique, ovary post-acetabular, on right side, vitellaria relatively more anterior to blind ends of caeca, attenuated body *G. ATTENUATUM*

SUMMARY

1. A new species, *Ganeo bufonis*, from a toad, *Bufo viridis*, in Kashmir, is described. This is the first species of the genus recorded from a toad; it differs from the known species in having both the vitelline glands confined to one side. The uterine coils do not extend into the post-caecal area; the excretory bladder is without any median stem and the metraterm is present.

2. *Ganeo tigrinum* Mehra and Negi, 1928 is also recorded for the first time from *Bufo viridis*. *Ganeo kumaonensis* Pande, 1937 and *Ganeo lingnanensis* Li, 1938 are both regarded as synonyms of *Ganeo tigrinum*.

3. A revised generic diagnosis and a key to the species of the genus *Ganeo* Klein, 1905 are given.

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On a New Species of the Genus *Cosmocerca* Diesing, 1861 from a Toad, *Bufo viridis*, in Kashmir*

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*From the Department of Parasitology, London School of Hygiene and
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COSMOCERCIDAE Travassos, 1925

COSMOCERCINAE Railliet, 1916

Cosmocerca Diesing, 1861

Cosmocerca kashmirensis n.sp.

The worms are slender, medium sized and attenuated at both ends. The cuticle is smooth. The lateral alae are narrow and extend from the anterior third of the oesophagus to the region of the plectanes in the male, but in the female they extend beyond the anus, terminating a short distance in front of the caudal tip.

The mouth is surrounded by three small lips, each provided with two papillae. The short "pharynx" is not well differentiated from the anterior end of the oesophagus. The cylindrical part of the oesophagus is followed by a well developed sub-globular and valvulated bulb. At the base of the lips, near the oesophagus, there are three small rod-shaped chitinized elements. The excretory pore is anterior to the bulb and is surrounded on one side by a semicircle of small rod-like refractile structures. The nerve ring is at about the middle of the oesophagus. The tail is tapering in both sexes, being shorter in length in the male.

The male : The plectanes are rosette-shaped and pre-cloacal in position. Each rosette has a central papilla which is surrounded by two concentric rings of cuticular tubercles. Each of these rings consists of 14—18 tubercles, those of the outer ring being larger than those of the inner one. Of the total of 19 plectanes, 16 are arranged ventrally in two irregular rows which terminate immediately in front of the cloacal opening. Some of these plectanes are shifted

* Part of a thesis approved by the University of London for the award of the M.Sc. degree.

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from their respective rows in such a way as to give the impression of four rows. The remaining 3 plectanes are not included in the two rows. They are slightly smaller and devoid of sub-cuticular thickening. Two of these are also ventral but placed obliquely a short distance anterior to the commencement of the two rows. The third additional plectane is laterally placed in front of the left lateral ala.

Besides the plectanes, numerous small papillae are present in the pre- and post-cloacal region of the male caudal end. The post-cloacal papillae are somewhat irregularly distributed and their arrangement may be roughly summed up as : 5 pairs ventral, 4 pairs dorsal, a single pair near the caudal tip and several unpaired and very small papillae scattered in the remaining post-cloacal area. The pre-cloacal papillae are arranged in two sub-ventral rows, extended a short distance anterior to the commencement of the plectanes, beyond which they become very small and indistinct. A few very small pre-cloacal papillae are also present outside the two sub-ventral rows. The body papillae in the anterior third of the body length are irregularly spaced and mainly arranged in the dorsal and ventral aspects. They tend to become very small and indistinct in the middle third of the body.

The two well developed spicules are equal in size and similar in shape. They are bent near the proximal end of the gubernaculum. The latter is triangular in shape and is heavily chitinized at the margins.

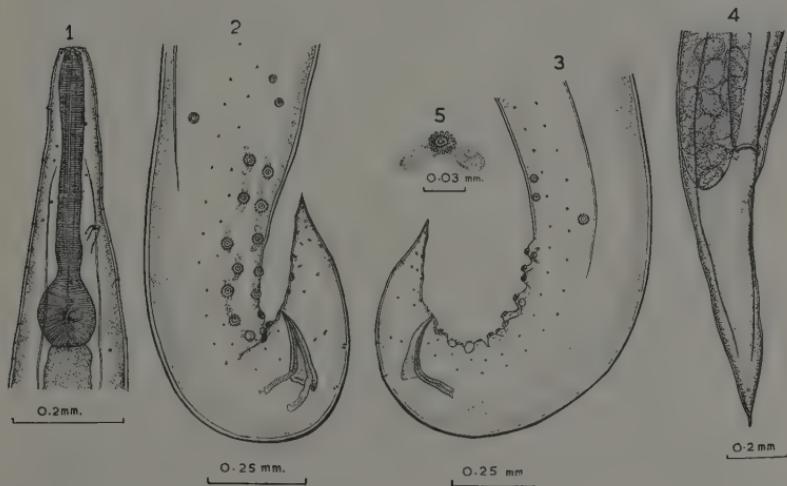
Measurements in mm.: Body length 4.3–5.5 ; breadth 0.36–0.41 ; oesophagus length including bulb 0.54–0.59 ; oesophageal bulb 0.14–0.15 × 0.13–0.14 ; head—excretory pore distance 0.34 ; head—nerve ring distance 0.27 ; tail length 0.3–0.33 ; spicule length 0.275–0.285 ; gubernaculum length 0.225–0.232 ; lateral alae maximum width 0.019–0.021.

The female : The females are longer. The vulva is located at the middle of the body length. The genital system is prodelphic. The uteri are compactly filled with large ovoid and apparently unsegmented eggs. The tail end is not differentiated into a caudal spine or a filament. The same is true of the male tail.

Measurements in mm.: Body length 4.7–7.6 ; breadth at vulva 0.33–0.54 ; oesophagus length including bulb 0.57–0.67 ; oesophageal bulb 0.15–0.18 × 0.12–0.16 ; head—excretory pore distance 0.32–0.53 ; head—nerve ring distance 0.29–0.30 ; tail length 0.5–0.9 ; head—vulva distance 2.3–3.8 ; eggs 0.075–0.112 × 0.060–0.075 ; lateral alae maximum width 0.019–0.027, terminating at 0.15–0.22 from the caudal tip.

RELATIONSHIPS

The present form differs from all the known species of the genus *Cosmocerca* in the number and arrangement of the plectanes. It is further characterized by its smooth cuticle, a poorly differentiated anterior pharynx, well developed and heavily chitinized spicules and gubernaculum and the absence of a distinct caudal spine in both sexes.



Cosmocerca kashmirensis sp. nov.

Fig. 1.—Lateral view of male anterior end. Fig. 2.—Ventro-lateral view of male caudal end. Fig. 3.—Lateral view of male caudal end. Fig. 4.—Lateral view of female caudal end. Fig. 5.—Plectane.

Of the total of 19 plectanes in the present species, three plectanes are simple rosettes being without any sub-cuticular thickenings. Two of them are also ventral and pre-cloacal like the remaining 16 and the third one is lateral and pre-cloacal. These "additional plectanes" are also present in four other species of *Cosmocerca*: *C. ornata* (Dujardin, 1845) Railliet and Henry, 1916, *C. trispinosa* Railliet and Henry, 1916, *C. brasiliense* Travassos, 1925 and *C. uruguayensis* Lent and Freitas, 1948. The present form differs from all the four species in the total number of plectanes, in the position of these "additional plectanes", and in the relative size of the spicules and the gubernaculum.

The spicules and the gubernaculum of the present form are well developed, heavily chitinized and large in size as compared with those in the majority of the *Cosmocerca* species. The largest sized spicules and gubernaculum are present in *C. timofejevoi* Skarbilovich, 1950 from which the present form differs in the number and the arrangement of the plectanes and the caudal papillae. From the drawing of the anterior region of *C. timofejevoi*, it appears that here the body papillae are also different in having the shape of minute rosettes. *C. commutata* (Diesing, 1851) Diesing, 1861, in which the spicules and the gubernaculum are also fairly well developed, differs from the present form in the number and the arrangement of the plectanes.

On the basis of the differences from the existing species of the genus, the present form is evidently a new species, to which the name *Cosmocerca kashmirensis* is given.

Host : *Bufo viridis*.

Habitat : Rectum.

Locality : Srinagar, Kashmir.

Type : Deposited in the Department of Parasitology, London School of Hygiene and Tropical Medicine.

DISCUSSION

C. australiensis and *C. propinquua* Johnston and Simpson, 1943, of which only the females are known, differ so widely from the females of the genus *Cosmocerca* that it appears doubtful if it is correct to include them in this genus. In the absence of the males, it is equally difficult to assign them to any of the known genera of Cosmocercidae. In *C. australiensis* the vulva is located a short distance behind the oesophageal bulb, the excretory pore is immediately anterior to the vulva, the oesophagus is very small, the eggs are comparatively much longer than broad and the genitalia are differently disposed. Similarly in *C. propinquua*, closely allied to the former species, the vulva is shifted still further anterior, being placed anterior to the oesophageal bulb—a character not present in the species of the genus *Cosmocerca*.

Including the present new species and the two doubtful species referred above, the total number of species in the genus *Cosmocerca* comes to seventeen. *C. kashmirensis* is the first record of the genus *Cosmocerca* from India. From a closely related genus, *Cosmocercoides*, Karve (1944) described *C. bufonis* from an Indian toad, *Bufo himalayanum*.

Remarks on some genera related to Cosmocerca.

Apart from *Cosmocerca* plectanes are also present in three other related genera, *Cosmocercoides* Wilkie, 1930, *Cosmocercella* Steiner, 1924 and *Paracosmocerca* Kung and Wu, 1945. Of these three genera, the plectanes of the genus *Cosmocercoides* are somewhat different in having no surrounding sub-cuticular thickenings and are given the name of "compound caudal papillae". Wilkie (1930) proposed the genus mainly on the basis of this difference from *Cosmocerca*. As already stated, the "additional plectanes" of *C. kashmirensis* n.sp. and four other species of *Cosmocerca* do not have sub-cuticular thickenings and in this respect resemble the compound caudal papillae of *Cosmocercoides*. The presence of both true plectanes and so-called "compound caudal papillae" in these species of *Cosmocerca* shows how closely the two genera are related to each other.

Due to the close resemblance between the plectanes of *Cosmocerca* and the compound caudal papillae of *Cosmocercoides*, several species were described in the former genus and later transferred to the latter genus. *C. dukae* Holl, 1928, as suggested by Wilkie (1930), was transferred to *Cosmocercoides* by Travassos (1931). *Oxysomatium variabilis* Harwood, 1930, regarded as the synonym of *C. dukae*, was transferred to *Cosmocercoides* by Travassos (1931). Hsü (1932) and Walton (1933) also regarded this species as a member of the genus *Cosmocercoides*. Chitwood (1933) regarded the genus *Trionchonema* Kreis, 1932 as a synonym of *Cosmocercoides* and transferred *T. rusticum* Kreis, 1932 to the latter. Similarly Skrjabin (1951) listed *Cosmocerca skrjabini* Ivanizki, 1940 in the genus *Cosmocercoides* on the basis of the presence of the compound caudal papillae.

The genus *Paracosmocerca* and its only species *P. mucronata* Kung and Wu, 1945 is differentiated from *Cosmocerca* on the basis of the absence of gubernaculum and the presence of peculiar fused spicules.

The genus *Cosmocercella* is characterized by the presence of a cuticular expansion or "bursa" at the level of the male anal opening as described by Steiner (1924) for its type, *Cosmocercella haberi*. *Cosmocerca banyulensis* also possesses a cuticular expansion in its male caudal end and should have been included in the genus *Cosmocercella*, but its authors, Chabaud and Campana-Rouget (1955) prefer to place it in *Cosmocerca*. They refer to the second species of *Cosmocercella*, *C. neveri* Hsü and Hoepli, 1933, in which the said cuticular expansion is not described. Hsü and Hoepli, at the end of the description of the male of *C. neveri* (page 161) write: "We are unable to make a definite statement regarding the lateral cuticular

expansion at the level of the anal opening, the so-called vesiculated bubble-shaped bursa, as described by Steiner for *C. haberii*, and are of the opinion that future examinations of more specimens regarding this morphological peculiarity are necessary." If this statement also implies the absence of the cuticular expansion in *C. neveri*, it should be regarded as a member of the genus *Cosmocerca*. Chabaud and Campana-Rouget, while eliminating the presence of the "bursa" as the characteristic feature of *Cosmocercella*, refer to the well developed spicules and reduced gubernaculum as the characters differentiating it from *Cosmocerca*. The latter genus, according to them, has the reverse characters : reduced or stunted spicules and well developed gubernaculum. But these characters are not valid for all the species of *Cosmocerca* in differentiating them from *Cosmocercella*. *Cosmocerca commutata*, *C. timofejevoi* and *C. kashmirensis* have both spicules and gubernaculum equally well developed. Similarly, there are several species of *Cosmocerca* which show other variations in the development of the spicules and the gubernaculum : *C. japonica* has reduced spicules but the gubernaculum is also apparently reduced or absent ; in *C. chilensis*, *C. parva* and *C. uruguayensis*, the spicules and the gubernaculum are more or less equal in size. It is hence concluded that if the genus *Cosmocercella* has to be retained as a genus distinct from *Cosmocerca*, it should continue to be characterised by the presence of the cuticular velum or "bursa". *C. banyulensis* should accordingly be considered as a member of the genus *Cosmocercella*.

List of Species of Cosmocera.

Following is a list of the existing species of the genus *Cosmocerca* along with their brief distinguishing features, hosts and distribution :—

1. *C. trispinosa* Railliet and Henry, 1916.

Syn. *Oxyuris ornata* Walter, 1856. nec. Dujardin, 1845.

Cosmocerca ornata (Walter, 1856) Diesing, 1861.

Three tipped tail in both sexes ; 13—14 pairs of plectanes in 4 rows, 2—3 post cloacal "plectanes".

Intestine of *Triturus alpestris*. Europe.

2. *C. brasiliense* Travassos, 1925.

9—11 pairs of plectanes in 2 rows, 5 pairs of small "additional plectanes" of which 3 pairs pre-cloacal and 2 pairs post-cloacal ; body papillae in lateral aspects.

Large intestine of *Bufo crucifer*, *Hyla faber*, *Hyloides güentheri*, *H. miliaris*, *Eleutherodactylus gollmeri*. Brazil.

3. *C. chilensis* Lent and Freitas, 1948.

6 pairs of plectanes in 2 rows; lateral alae absent. (Females unknown).

Rectum of *Rhinoderma darwini*. Chile.

4. *C. commutata* Diesing (1851) Diesing, 1861.

Syn. *Ascaris commutata* Diesing, 1851.

Oxyuris ornata Weinland, 1859.

Nematoxys commutatus (Diesing, 1851) v. Linstow, 1889.

14 pairs of plectanes in 2 rows; conical tail.

Intestine of *Rana esculenta*, *R. temporaria*, *Bufo viridis*, *B. bufo*, *Hyla arborea*, *Pelobates fuscus*, *Salamandra atra*, *S. salamandra*, *Bombina bombina* and *Triturus cristatus*. Europe. *Bufo marinus*, *Hyla luteus* (?), *H. tschudii* (?), and *Leptodactylus typhonius*. Brazil.

5. *C. japonica* Yamaguti, 1938.

5 pairs of plectanes, each with a semi-circular crown of 6 tubercles; single spicule with 2 segments; excretory pore bulbar or slightly post-bulbar; 6 longitudinal rows of body papillae in male and 4 rows in female; caudal filament in both sexes, in female with 2 lateral spines.

Rectum of *Rana nigromaculata*, *R. rugulosa*, *R. japonica*, *Hyla arborea japonica*. Japan.

6. *C. kashmirensis* n.sp.

19 plectanes of which 8 pairs in 2 irregular rows and 3 additional plectanes, 2 ventral and one lateral; smooth cuticle; caudal filament absent in both sexes.

Rectum of *Bufo viridis*. Kashmir.

7. *C. limnodynastes* Johnston and Simpson, 1943.

11 plectanes of which 5 pairs in 2 rows and one median, anterior to cloaca; gubernaculum spicule-shaped; excretory pore bulbar; ventral wall of pharynx prolonged between ventro-lateral lips to resemble so-called fourth lip.

Intestine of *Limnodynastes dorsalis*. South Australia.

8. *C. longicauda* (v. Linstow, 1885) Railliet and Henry, 1916.

Syn. *Nematoxys longicauda* v. Linstow, 1885.

6 pairs of plectanes in 2 rows, each plectane with 4-6 tubercles; excretory pore post-bulbar; body papillae in longitudinal rows; female tail with 2 papillae.

Intestine of *Triturus alpestris*, *T. cristatus* and *T. vulgaris*. Europe.

9. *C. minuscula* Travassos, 1931.

5 pairs of plectanes in 2 rows, each with an incomplete ring of tubercles; reduced spicules; 2 longitudinal series of body papillae. (Females not known).

Large intestine of *Rana temporaria*. Europe.

10. *C. ornata* (Dujardin, 1845) Railliet and Henry, 1916.

Syn. *Oxyuris ornata* Dujardin, 1845, nec. Walter, 1856 nec. Diesing, 1861.

Nematoxys ornatus (Dujardin, 1845) Schneider, 1866.

5-8 pairs of plectanes in 2-4 rows, 2 pairs of post-cloacal small additional plectanes; body papillae in longitudinal series; one pair of papillae in the middle of female caudal filament.

Intestine of *Rana esculenta*, *R. temporaria*, *Bufo bufo*, *B. viridis*, *B. vulgaris*, *Triturus alpestris* and *T. cristatus*. Europe.

11. *C. parva* Travassos, 1925.

5 pairs of plectanes in 2 rows and terminate relatively more anterior to the cloacal opening; 2 series of body papillae.

Intestine of *Elosia nasus*. Brazil.

12. **C. pulcherrima* Ivanizki, 1940.

8 pairs of plectanes in 2 rows; spicules probably reduced. (Females not known).

Intestine of *Bufo viridis*. U.S.S.R.

13. *C. timofejevoi* Skarbilovich, 1950.

8-10 pairs of plectanes in 2 rows; well developed spicules and gubernaculum, bearing the largest size among the existing species of the genus; body papillae present.

Intestine of *Rana* sp. and *Bufo* sp. U.S.S.R.

14. *C. uruguayensis* Lent and Freitas, 1948.

7 pairs of plectanes in 2 rows, one small additional plectane post-cloacal; lateral alae absent; excretory pore bulbar. (Females not known.)

Intestine of *Ceratophrys americana*. Uruguay, South America.

15. †*C. banyulensis* Chabaud and Campana-Rouget, 1955.

11 plectanes in 2 rows; cuticular velum behind cloaca extending to last pair of post-cloacal papillae; spicules reduced; body papillae present.

Rectum of *Rana ridibunda*. Banyuls. France.

16. †*C. australiensis* Johnston and Simpson, 1943.

Vulva short distance behind oesophageal bulb; excretory pore post-bulbar and immediately anterior to vulva; divergent ovaries arise near middle of body; eggs ellipsoidal, relatively more longer than broad. (Males not known.)

Intestine of *Limnodynastes dorsalis*. South Australia.

17. †*C. propinquua* Johnston and Simpson, 1943.

Vulva anterior to oesophageal bulb; both ovaries in posterior half of body. (Males not known.)

Intestine of *Limnodynastes dorsalis*. South Australia.

SUMMARY

1. A new species, *Cosmocerca kashmirensis* n.sp. from the toad, *Bufo viridis*, in Kashmir, is described. The new species has 19 plectanes in the male tail, of which 3 plectanes are simple rosettes and resemble the compound caudal papillae of the genus *Cosmocercoides*.

2. The existing species of the genus *Cosmocerca* Diesing, 1861 are listed and briefly described.

ACKNOWLEDGMENTS

I am grateful to Prof. J. J. C. Buckley, under whose supervision this work was carried out. I am also thankful to Dr. L. S. Yeh for constructive criticism and suggestions, and to Mr. G. Inglis of the British Museum (Nat. Hist.) for providing facilities for the study of some type material in the Museum.

* Original reference not available. Brief characters and measurements given by Skarbilovich (1950).

† Probably belongs to the genus *Cosmocercella*.

‡ Generic name doubtful.

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***Capsulata edenensis* gen. et sp. nov., a New Cestode with an Unusual Type of Growth, from *Limosa lapponica* (L.); with Systematic Notes on the Genera *Southwellia* Moghe, 1925 and *Malika* Woodland, 1929**

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***CAPSULATA EDENENSIS* gen. et sp. nov.**

Host : *Limosa lapponica* (Linn. 1758)

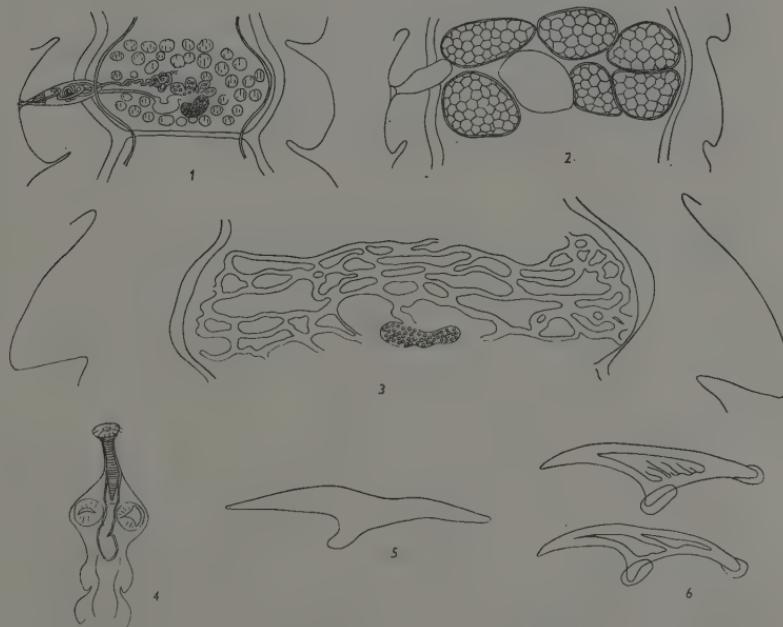
Locality : The estuary of the River Eden, Fife, Scotland.

Description : The specimens were collected from three Bar-tailed Godwits shot in the winters of 1956 and 1957. The description below applies mainly to the first infestation found. There are certain differences between the infestations which are noted later. There were up to 150 individuals in each infestation, varying from immature worms consisting of a scolex and a few proglottides to mature strobilas containing some 300 segments and reaching a length of 75 mm. The maximum breadth of the strobila is 1.8 mm. The onset of maturity is accompanied by a marked increase in the breadth of the strobila and the mature proglottides are broader than long.

The scolex (Fig. 4) has a diameter of 200-280 μ and a length, including neck and rostellum, of 580-730 μ . The rostellum, of length up to 300 μ and diameter of 30-50 μ at the base, bears 16 hooks (Fig. 5) of length 37-45 μ in two slightly separated rows. The hooks are the same size in the two crowns. The suckers face forward slightly and have a diameter of 90-120 μ . The neck is very short, of length 175 μ and breadth 160 μ . The genital apertures are unilateral and situated in the middle of the length of the proglottis. The genital ducts pass between the longitudinal excretory vessels. The vagina opens in the genital atrium ventrally, and occasionally slightly postero-ventrally, to the cirrus-sac. It runs, parallel to the

cirrus-sac but in a ventral position, towards the centre of the proglottis. There are 30–45 testes completely surrounding the female glands, the greater bulk of them lying anterior and lateral to the female glands. The testes reach a size of 50–60 μ in the more mature proglottides. The cirrus-sac, which is 100–185 μ long by 52–75 μ , extends beyond the longitudinal excretory canals. It contains a much coiled ductus ejaculatorius. The cirrus is short, of length about 40 μ and diameter 10 μ , and is covered with many tiny spines. The distal portion of the cirrus-sac has an internal lining of cells which are probably myoblasts. The vas deferens runs from the cirrus-sac towards the centre of the proglottis, where it is coiled in an area slightly poral to the female glands. There is no external or internal seminal vesicle but the vas deferens and the ductus ejaculatorius become expanded with sperms in the mature proglottides and probably function as such. The female glands are in the posterior half of the proglottis. The ovary consists of from 4 to 9 separated round lobes situated in a semicircle round the vitelline gland. The vitelline gland is situated behind the ovary, it is compact and may be slightly lobed. In mature segments a dorsal loop of the vagina is expanded to form a very large receptaculum seminis. It reaches a size of 350 by 270 μ and dominates the centre of the gravid proglottis. The vagina is ventral to the cirrus-sac and is a wide tube, of diameter 24–38 μ ; its wall is composed partly of what appear to be glandular cells. The uterus is first formed as a reticulum (Fig. 3) extending forward from the female glands, and occupying, in a ventral position, an area anterior and lateral to the ovary and vitelline gland. Later the uterus becomes filled with eggs and occupies the whole ventral part of the medulla. Some portions of the network seem to be more expanded with eggs and it is these regions that probably develop into capsules. The gravid proglottides contain from 4 to 15 egg capsules each containing 40–120 eggs. The egg capsules vary in size from 115×160 μ to 270×400 μ , the largest being found in those segments with fewer capsules. The egg capsules are liberated by laceration of the gravid proglottides and many were found free in the intestinal contents of the hosts of two of the infestations. The wall of the capsule, in the early stages, is a syncytium derived from the single layer of cells of which the uterine wall is composed. Later, the inner and outer surfaces of the syncytial layer become thickened, and the wall of the capsule has the appearance of being composed of a single non-living layer except where the two surfaces are separated by the remains of a nucleus. In the liberated condition the capsule wall is thin, about 1 μ thick, and appears to be a single layer of non-living material. The eggs are round, or, due to the natural pressures from the neighbouring eggs, polygonal. They have

a diameter of 36–45 μ . The onchospheres have a diameter of 30–42 μ . The lateral onchosphere hooks are of two different sizes, 17 μ and 19 μ and the medial hooks have a length of about 22 μ .



Capsulata edenensis n.gen., n.sp.

Fig. 1.—Mature proglottis. Fig. 2.—Gravid proglottis. Fig. 3.—Mature proglottis, showing the reticulate uterus soon after its formation. Fig. 4.—Scolex. Fig. 5.—Rostellar hook.

Malika odhneri (Fuhrmann, 1909)

Fig. 6.—Rostellar hooks.

There are two layers of longitudinal muscle fibres, the inner is composed of 50–60 bundles each with 10–20 fibres and the outer layer consists of small bundles or of single fibres. Transverse fibres are absent except for a single bundle of fibres at the anterior margin

of the proglottis. The fibres of which this transverse bundle is composed arise from the lateral longitudinal fibres and from the subcortical layer at the anterior lateral border of the segment. These transverse fibres are internal in relation to the longitudinal fibres.

Anatomical differences were noted between specimens from different infestations. In the first infestation the gravid segments contain 4-8 egg capsules, in the other two infestations there were 7-15 egg capsules per segment. In the first infestation the ovary has 4-7 lobes, while in the other infestations the ovary has 5-9 lobes. There was also a slight variation in hook size, 41-44 μ in the first infestation and 37-39.6 μ in the other infestations.

Systematics and notes on the new species and on the related genera
Southwellia Moghe, 1925 and *Malika* Woodland, 1929

The described species approaches most nearly to three genera ; *Southwellia* Moghe, 1925, *Malika* Woodland, 1929 and *Similuncinus* Johnston, 1909 all of which have unilateral genital apertures and "egg capsules" containing several eggs.

Southwellia Moghe, 1925

This genus has contained two species : *Southwellia ransomi* Chapin, 1926 which is a synonym of *Dilepis undula* (Schrank, 1788), vide Fuhrmann, 1932, and *Southwellia gallinarum* (Southwell, 1929). I have examined the types of this last species and am in full accordance with the findings of Baer (1957). Egg capsules are not formed, the uterus is persistent as a reticulum which extends laterally to fill completely the medulla of the proglottis. In the oldest segments when the uterus is swollen with eggs, small lobes may be forced out between the longitudinal muscle fibres ; these lobes have the appearance of egg capsules. The tubular uterus, when doubled back on itself may also have been mistaken for egg capsules. The cirrus-sac of *Southwellia gallinarum* is long (about 650 μ) and reaches almost to the centre of the proglottis. In view of the structure of its uterus, this species should be transferred to the genus *Dilepis* Weinland, 1858, it becomes *Dilepis gallinarum* (Southwell, 1921) and the genus *Southwellia* Moghe, 1925 lapses into synonymy with *Dilepis* Weinland, 1858.

Malika Woodland, 1929

The genus *Malika* Woodland, 1929 has one inconsistency which should be mentioned. The definition of the genus takes the form, following Fuhrmann (1932) for example, "Dipyliidiinés avec rostre armé d'une couronne de crochets". However Woodland in his original paper did not stipulate the number of rows of hooks. Examination of the types of *Malika oedicnemus* in the British Museum left me with no doubt that there are actually two rows of hooks. Thus any definition of the genus which stipulates the number of rows of hooks as one is not acceptable.

Malika Woodland, 1929 at the present time contains 6 species : *Malika oedicnemus* Woodland, 1929 ; *Malika pitiae* Inamdar, 1933 ; *Malika kalawewaensis* Burt, 1940 ; *Malika himantopodis* Burt, 1940 ; *Malika zeylanica* Burt, 1940 and *Malika skrjabini* Krotov, 1953. I have had the opportunity of examining Burt's Ceylon material, and my findings for the hook characteristics of these specimens are recorded in the Table I below with those of *Malika oedicnemus* Woodland, 1929 and *Dilepis odhneri* Fuhrmann, 1909. The figures given in brackets are those of the original author, other figures are personal observations.

TABLE I

	Hook No.	Hook Size
<i>Dilepis odhneri</i> Fuhrmann, 1909	30 (32)	76-84.5 μ (70-80 μ)
<i>Malika oedicnemus</i> Woodland, 1929	— (30)	— (73 μ)
<i>Malika kalawewaensis</i> Burt, 1940	30 (26-28)	76-80 μ (58 μ)
<i>Malika himantopodis</i> Burt, 1940	32 (30)	76-80.5 μ (73-75 μ)
<i>Malika zeylanica</i> Burt, 1940	30 (32)	75-79.5 μ (76-83 μ)

Scolices of this material were mounted and crushed in Berlese fluid. This procedure enables the hooks to be seen clearly so that accurate drawings and measurements can more easily be made. The results recorded above emphasize the importance of mounting hooks so that they can be seen clearly. The original determination of the hook characteristics of these species was from whole mounts in balsam, and in the case of *Malika kalawewaensis*, from a single scolex with its rostellum invaginated. The hooks of these three species are identical in shape (Fig. 6) and their dimensions are well within the range to be expected from different infestations of the same species. Formerly, these three species could be separated by differences in the number and size of the hooks (Burt, 1940), but as these three species can no longer be distinguished by their hook characteristics, the slight differences in anatomical detail are not in themselves sufficient to separate them as species.

I did not have the opportunity of examining a scolex of *Malika oedicnemus* in Berlese but the original figures of the hooks of this species and those for example of *M. zeylanica* from balsam mounts are similar. Burt separated his species from *M. oedicnemus* mainly on the grounds that the latter species has only one row of hooks. As *Malika oedicnemus* has in fact two rows of hooks these four species should be considered as synonymous. The deviation in anatomical detail of the form described as *M. himantopodis* may be due to its occurrence in another, possibly accidental, host (*M. himantopodis* was described from a Stilt, the others from Stone Curlews).

Dilepis odhneri Fuhrmann, 1909 has been recorded from the White Nile (Fuhrmann, 1909) and from Omo-Sagan (Fuhrmann and Baer, 1943). The material is in a highly contracted condition and does not contain gravid segments, but it is possible to see that the anatomy as well as the hook characteristics correspond with the Indian and Ceylon material discussed earlier. Thus we come to the conclusion that these five species are synonymous. The first description was under the name *Dilepis odhneri* Fuhrmann, 1909, accordingly, as the genus *Malika* is retained, the type species should be designated *Malika odhneri* (Fuhrmann, 1909) with the following synonyms: *Dilepis odhneri* Fuhrmann, 1909; *Malika oedicnemus* Woodland, 1929; *Malika kalawewaensis* Burt, 1940; *Malika himantopodis* Burt, 1940 and *Malika zeylanica* Burt, 1940.

Also attributed to the genus *Malika* Woodland, 1929 are the species *M. pittae* Inamdar, 1933 and *M. skrjabini* Krotov, 1953. Little is known of the parasites from the group of hosts (Pittidae) in which the former species was found, and although *M. pittae* seems to bear little relationship to the type of the genus, it should remain in that genus until re-examined or more material is investigated. *M. skrjabini* on the other hand, from *Limosa limosa melanurooides* Gould bears a very close resemblance to *Dilepis limosa* Fuhrmann, 1907 recorded from a different sub-species of the same host and also from the U.S.S.R. (Kholodkovsky, 1912 and Dubinina, 1953). The two forms have the same wide strobila which is characteristic for *Dilepis limosa* and almost unique for dilepid tapeworms from Charadriiformes. The hooks have the same shape and are within the same range for number and size (*M. skrjabini* 16-22 hooks, 81-124 μ and *D. limosa* 20 hooks, 99-110 μ). In *D. limosa* the hooks are distributed in two crowns while in *M. skrjabini* the number of rows of hooks is not stipulated. A character of the genus *Malika* is that the genital canals pass between the longitudinal excretory

vessels. *Malika skrjabini* is described as having the genital canals passing ventrally to the excretory vessels (although the dorsal canal is given as the wider of the two) and in this respect approaches nearer to the genus *Dilepis* which has the genital canals passing to one side of the excretory vessels. The anatomy is identical for the two species *M. skrjabini* and *D. limosa* except as regards the structure of the cirrus-sac and uterus. The type specimens of *D. limosa* have a very long cirrus-sac (790–870 μ), examples of this species from the U.S.S.R. are described as having a cirrus-sac which extends beyond the excretory canals (Dubinin, 1953), and *M. skrjabini* is described as having a cirrus-sac (138 μ by 179 μ) which does not normally reach the excretory vessels. The cirrus-sac of the type specimens of *D. limosa* is long and narrow, and in contracted material it is difficult to see where it ends and where the vas deferens begins, as they are of similar diameters and are obscured by the overhang of the posterior end of the preceding segment. The uterus of *M. skrjabini* is described as being reticulate, later becoming constricted off into egg capsules, while the uterus of *D. limosa* is reticulate but does not form egg capsules. In the type specimens of *D. limosa* however, the gravid uterus has the appearance of being strongly lobed or at times having the appearance of egg capsules. It is important to note that the uterus of *Dilepis undula* (Schrank, 1788), the type species of the genus *Dilepis*, is reticulate "though in whole mounts it appears to be broken up into capsules, each containing several eggs, accurate examination of serial sections reveals that each lobe is in communication with the rest of the uterus", (Davies, 1935). *Dilepis gallinarum* (Southwell, 1929) was erroneously described as having a short cirrus-sac and egg capsules and one cannot preclude the possibility that the same mistake could have been made in this instance with *M. skrjabini*. Apart from these two discrepancies, the description of *Malika skrjabini* Krotov, 1953 makes it clear that this species is in fact a synonym of *Dilepis limosa* Fuhrmann, 1907.

The species that I have described has dilepid hooks and egg capsules and therefore belongs to the sub-family Dipyliidae (Stiles, 1896). It bears some relationship to the genus *Similuncinus* Johnston, 1909 but is distinguished from this genus by the difference in the relative positions of the genital canals and the excretory vessels.* It approaches nearest to the genus *Malika* Woodland,

*There is some confusion in the description of the type species of the genus, *Similuncinus dacelonis* Johnston, 1909. The genital ducts are described as passing ventrally to the excretory canals while at the same time the dorsal vessels are the larger and possess the transverse connection. The general anatomy and the form of the uterus [reticulate, with the eggs later lying in groups in the parenchyma (Johnston, 1909)] make it possible that *Similuncinus* is another synonym of *Dilepis*.

1929 which has egg capsules containing several eggs and genital ducts passing between the longitudinal excretory canals. The new species differs from the genus *Malika* in two fundamental ways. The new species has female glands posterior in the segment and testes mainly anterior, whereas in *Malika* the female glands are anterior and the testes posterior in position. The uterus is at first reticulate, as in the genus *Dilepis*, but egg capsules are formed and actually released into the intestine of the host. In *Malika* on the other hand, the uterus is at first sac-like, it later becomes lobed and constricted off into egg capsules.

The described form, while being placed in the sub-family Dipyliidae (Stiles, 1896) has an anatomy which bears a similarity to that of certain Davainiids, but its hook characteristics of course preclude the possibility of its being included in that group. The release of egg capsules, an outstanding feature of this species, has been described from a *Hymenolepis* by Joyeux and Baer (1955). These capsules are somewhat similar in this instance but they have a different mode of formation and are from a relatively distant group of tapeworms so do not have much bearing on the species described. The anatomy of members of the genus *Dipylidium* Leuckart, 1863 has many characters in common with that of the present form. In both the testes are numerous and are situated anterior and posterior to the female glands, the vagina in *Dipylidium* sometimes opens ventrally to the cirrus-sac, and the uterus is reticulate and later breaks down into egg capsules containing several eggs. The double genitalia and the hook characteristics are however very different from the species that I have described, but it would appear that the new species is a truer monopylidium than many of the other species that have been given this title at one time or another. As the new species differs from the other existing members of the sub-family Dipyliidae (Stiles, 1896) in certain fundamentals which have been outlined above, and as it also has an unusual type of growth which is described in the second half of this paper, a new genus is made which is designated *Capsulata* n.gen. The definition of the new genus is as follows :—

Capsulata n.gen.

Dipyliidae with dilepid hooks. Genitalia single. Female glands posterior in the segment. Testes surrounding the female glands, but mainly anterior. Genital pores unilateral. Genital ducts passing between the longitudinal excretory vessels. Vagina ventral to the cirrus-sac. Large receptaculum seminis. Uterus

reticulate, later forming egg capsules. Egg capsules few in number and each containing many eggs—Parasites of birds.

The new species that has been described above is given the name *Capsulata edenensis* n.gen., n.sp. and is designated the type species of the genus *Capsulata* n.gen.

Type host of *Capsulata edenensis* n.gen., n.sp. is *Limosa lapponica* (Linn.) and the type locality the estuary of the River Eden, Fife, Scotland.

The type material will eventually be deposited in the British Museum (Nat. Hist.).

A note on the growth of *Capsulata edenensis* n.gen., n.sp.

The following description refers mainly to the first infestation found. The infestation consisted of over a hundred individuals of this species situated in the duodenum, as well as an estimated 6,000 specimens of *Ophryocotyle proteus* Friis, 1869, the specimens of the latter species as well as being of much smaller size, were confined to the posterior part of the intestine. The specimens of *Capsulata edenensis* n.gen., n.sp. vary in length from 1 mm. to 70 mm. The smallest specimen (Fig. 8) consists of a scolex, a short neck, a single segment and a thicker posterior region. This posterior region has indentations which become closer together and less distinct as one proceeds towards the posterior end, the indentations disappear about half way along. Larger specimens (Figs. 9 and 10) have a greater number of distinct segments behind the scolex but the segments become more compressed together and less distinct as one proceeds towards the hind end, and signs of segmentation have disappeared completely in the last portion. In specimens 20–30 mm. long external segmentation disappears completely in the last 5–10 mm., but internal segmentation can be discerned in this region (Fig. 11). The genital anlage is also visible in the hindermost segments of this region. In still larger worms external segmentation becomes distinct along the whole length of the strobila, although not quite so pronounced towards the posterior end.

Further examination was made of 20 larger specimens, and measurements were made of the total number of segments, the distance from the scolex at which the genital anlage is discerned, the distance from the scolex at which maturity is apparent, the distance

from the scolex at which eggs are first seen in the uterus, and the maximum breadth and the length of the strobila. With respect to the position of anlage, the onset of maturity and the appearance of eggs in the uterus the distance is expressed as the number of segments from the scolex. The segments are deemed to be mature when their genital ducts become cuticularised, this takes place over one or two segments. The results are recorded in Table II.

In the discussion following certain assumptions have been made : firstly, that "length \times maximum breadth" of the strobila is a reasonable representation of the size of the specimen ; secondly, that the size is a function of the age of the specimen, as long as the worm is complete and has not shed any segments. In these specimens this last state can be seen from the character of the last segment ; it is either rounded if complete, or lacerated if segments have been lost. All the specimens represented in the table are deemed to be complete. The word "age" I have here used to refer to the stage of development reached, rather than in any absolute sense. In the figures the units of "length \times maximum breadth" are actually sq. mm., but this is of little importance as only the relative sizes of the worms are being compared.

1. The total number of segments.

The points on Fig. 12 lie in a more or less horizontal band. This indicates that the total number of segments is nearly constant within this size range of specimens.

2. The genital anlage (Fig. 12).

The genital anlage is confined to the relatively close limits of the 37th to the 51st segment behind the scolex regardless of the size of the strobila.

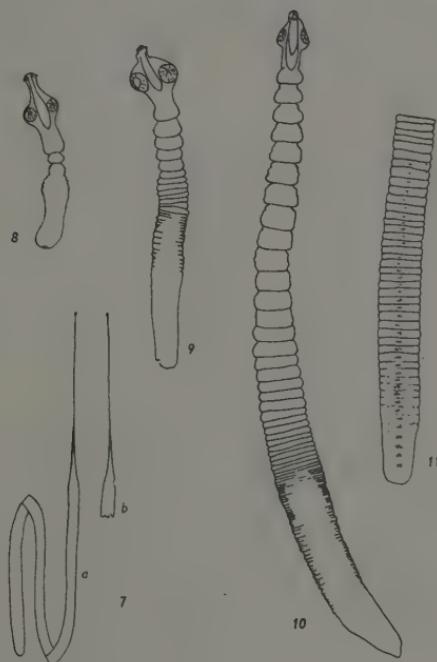
3. The position of the onset of maturity. (Fig. 13).

The results indicate that the distance from the scolex at which mature segments are found decreases with increase in size of the worm. Put in another way, the onset of maturity moves towards the scolex as the strobila ages, or alternatively, the number of mature segments is proportional to the age of the worm.

4. The appearance of eggs in the uterus (Fig. 13).

The same type of result as in the last case is found here. The commencement of the production of eggs in the strobila moves

towards the scolex as the worm ages, or alternatively, the number of gravid segments is proportional to the age of the strobila. It can be seen from this figure that the separation between the onset of maturity and the commencement of egg production becomes considerably less as the worm ages and that these approach very close to the genital anlage.



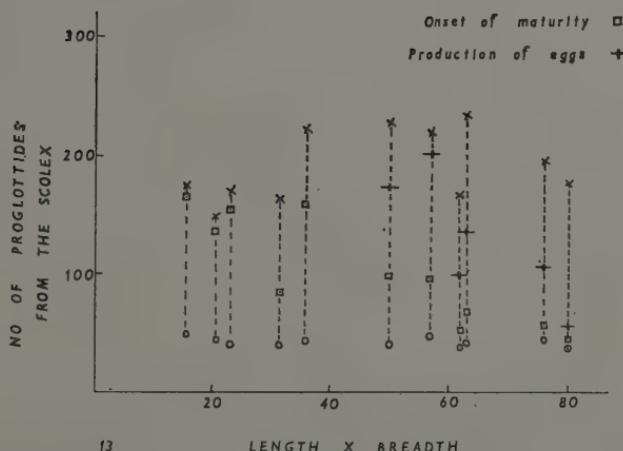
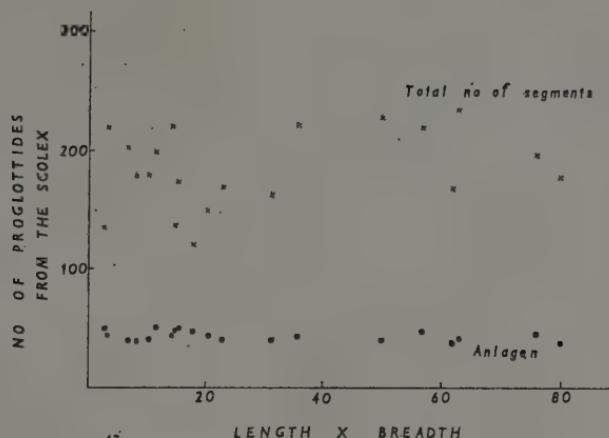
Capsulata edenensis n.gen., n.sp.

Fig. 7a.—Strobila before the gravid segments have been shed. Fig. 7b.—Strobila after the gravid segments have been shed. Fig. 8.—Young specimen, length 1 mm. Fig. 9.—Young specimen, length 1.8 mm. Fig. 10.—Young specimen, length 3.5 mm. Fig. 11.—Posterior end of a young specimen, length 21 mm.

From these results and the appearance of the younger specimens described earlier certain conclusions can be drawn as to the probable type of growth that this species undergoes. It can only be a probable sequence of events as the examples examined are a static cross-section of a growing population.

TABLE II

Number of specimen	Total No. of proglottides	Production of eggs	Onset of Maturity	Anlage	Length mm.	Max. breadth mm.	Length × Breadth
SI/C. 1	197	105	57	44	60	1·22	76
2	233	136	68	41	61	1·04	63
3	178	56	44	37	65	1·22	80
4	169	—	154	41	49	0·47	23
5	219	—	—	44	42	0·35	14·4
7	173	—	165	50	39	0·4	15·6
8	199	—	—	51	33	0·36	11·8
11	135	—	—	50	15	0·19	2·9
16	138	—	—	48	35	0·5	17·5
17	150	—	136	43	38	0·54	20·5
19	219	—	—	43	18	0·19	3·4
21	203	—	—	39	26	0·26	6·7
22	221	—	—	42	62	0·58	36
24	163	—	159	—	51	0·62	31·5
26	179	—	84	39	40	0·3	10·5
28	178	—	—	38	33	0·25	8·25
29	120	—	—	47	28	0·64	18
31	169	99	52	37	47	1·3	62
32	228	173	98	41	68	0·73	50
33	219	201	96	47	67	0·85	57



Capsulata edenensis n.gen., n.sp.

Fig. 12.—Distribution of the total number of segments and of the position of anlage for strobilas of different sizes. Fig. 13.—Distribution of the position of the onset of maturity and of the first production of eggs for strobilas of different sizes. The position of anlage and the total number of segments are also shown.

The figure showing the total number of segments indicates that this is more or less constant whatever the size of the strobila. When the actual difference in size of the strobila is considered this fact becomes more interesting. Thus a strobila 18 mm. long and with a maximum breadth of 190μ has about the same number of segments as a worm 65 mm. long and 1.2 mm. wide. The latter worm probably has a weight a hundred times that of the former, and the difference in size is similar to that between a piece of thread 2 cm. long and a 6.5 cm. length of shoelace. This constancy in the number of segments and the series of young specimens (Figs. 8-11) indicate that segmentation takes place when the worm is very small. There are three possible explanations that would account for the absence of segmentation of the posterior end of young strobila. Firstly, the young worms could be considered abnormal. Abnormality might be due to infestation of an unfavourable host; this is unlikely as this species was found in every specimen of the Bar-tailed Godwit that was examined and in no other Charadriiformes examined from the same locality. Abnormality could also be due to effects from overcrowding. This again seems unlikely as one of the hosts had a relatively small infestation yet still contained immature individuals as well as mature ones. It is also possible that abnormality could be due to an effect caused by successive infestations of the same host. The high rate of infestation and the size of infestation found indicate that this parasite of the Bar-tailed Godwit is fairly common in this locality and that multiple infestation is probably frequent. There is no argument against the possibility of abnormality being caused by multiple infestation, which no doubt occurs and which accounts partly for the many different stages of development of the worm found, but as these young stages were found in all of the hosts of this species examined, they appear to be the rule and not the exception.

The absence of segmentation at the posterior end of the young worms could also be explained by a growth sequence in which segmentation from the neck region takes place in a normal way, this being followed by its disappearance at the posterior end. However the short neck with well formed proglottides immediately behind it and the absence of the typical growth zone make this unlikely.

The third possibility is that in the young worms, between the stages represented by the worms shown in Figs. 8-10, segmentation takes place from a diffuse area in the hinder region of the body.

This process is relatively rapid and is complete, no further segments being formed in the later development of the worm.

These young individuals bear a slight resemblance to certain plerocercoid larvae. However, without knowing the whole life cycle of this species it is impossible to say what larval stages it undergoes. It is in fact very unlikely that this species has a plerocercoid larva. What must be emphasised is that the hind end of these young individuals, although being unsegmented at first, remains and eventually becomes segmented and develops to full maturity, whereas the corresponding part of a plerocercoid larva is lost.

Fig. 13 shows the relative positions along the worm of the genital anlage, the onset of maturity, the production of eggs and also the total number of segments in the worm. The positions of the onset of maturity and egg production become nearer to each other as the worm ages and they both approach the genital anlage. Thus in a strobila of length 65 mm. and maximum breadth 1.2 mm., anlage is at the 37th proglottis, the onset of maturity is at the 44th, and eggs are apparent 12 segments further on at the 56th proglottis from the scolex. This contrasts strongly with a young worm of a similar length, 67 mm., but with a smaller maximum breadth of 0.85 mm., which has its anlage at the 47th segment, onset of maturity at the 96th segment and eggs are produced at the 201st segment. Thus after segmentation and a period of growth in which this segmentation becomes asserted we can visualise a period in which the strobila increases in thickness and breadth but of greater importance is the maturation of the genitalia, this taking place at the posterior end first and working forward. The number of mature and gravid proglottides increases and the position of the onset of maturity and the production of eggs moves towards the scolex.

Curiously enough, the position of the anlage relative to the scolex is constant between narrow limits and the anlage does not move towards the scolex as the worm matures as one might expect from the behaviour of the position of the onset of maturity. This constancy of the position of the genital anlage is difficult to account for, but it could possibly be explained on a theory of axial gradients.

Further stages in development were not found in this host bird but examples from second and third hosts indicates what happens later. In appearance the specimens (Figs. 7a, b) are narrow for

40–50 proglottides then rapidly widen out to about 1·5 mm. This wide portion in some examples is very short and the hinder proglottides are lacerated and empty of egg capsules. A specimen such as this is obviously older than those described earlier had has shed most of its ripe proglottides. It may be noted here that even in this older stage there are some 40 or so narrow undeveloped segments. A worm like this has probably reached almost the end of its productive life.

To summarise the different stages in development that I have postulated :—

1. Segmentation, this takes place from a diffuse area in the posterior region of the young worm.
2. A period of material growth in which the worm increases in size, and gains complete external and internal segmentation. The posterior region of the strobila is the last to gain complete external segmentation.
3. Maturation of the sexual organs, this proceeds from the posterior end and works towards the scolex.
4. Loss of gravid segments from the posterior end, until 40–50 segments remain, at this stage the worm nears the end of its productive life.

The growth that I have described for *Capsulata edenensis* n.gen., n.sp. differs greatly from the classical picture of a tapeworm in which segments are produced at the neck region as fast as they are shed, when ripe, from the posterior end. Apolysis takes place in the new species in so much as ripe segments are shed from the posterior end. Its growth, however, differs from the classical picture in that the growth zone is not immediately behind the scolex, but is a diffuse region situated at the posterior end of the young strobila. Segmentation taking place from a region other than in the neck is by no means unknown among tapeworms. It is widespread among pseudophyllideans and has been recorded in some detail by Curtis (1906) in *Crossobothrium laciniatum* Linton, and by Fuhrmann (1925 and 1931) in *Idiogenes nana* (Fuhrmann) and *Haplobothrium globuliforme* Cooper. These last species however have additional complications in that they form primary and secondary individuals and their associated pseudoscolices. It is difficult to compare the new species with very distantly related pseudophyllideans, their anatomy is completely different and their segmentation is generally

not orderly although it also arises from a diffuse growth zone in the posterior region of the body. The growth of *Crossobothrium laciniatum* Linton as described by Curtis (1906) differs from *Capsulata edenensis* n.gen., n.sp. in that its growth zone is somewhere in the middle of the young strobila and gives off "anterior" and "posterior" segments. The strobila of the new species could be compared to the "anterior" segments of *Crossobothrium laciniatum* Linton.

Idiogenes nana (Fuhrmann) is the only other cyclophyllidean tapeworm, as far as I can ascertain, which shows this unusual type of growth. Related to its growth is the production of secondary individuals and the formation of pseudoscolices. If a single individual of this species is compared to a strobila of *Capsulata edenensis* then a certain similarity between the two may be seen. The segmentation of *Idiogenes nana* also appears to work backwards from the scolex end; "La strobilation se fait en effet en partant de l'extrémité qui porte le pseudoscolex et en se propageant de là en arrière (Fig. 3, a, b, c). De ce fait les derniers proglottis de l'extrémité distal seront les plus jeunes et non les plus âgés, comme chez la généralité des cestodes." In Fuhrmann's examples as well as mine the hindermost proglottides are the first to reach maturity, it may be thus questionable to state that the posterior segments are in any way younger than the anterior ones, although the latter may have gained their external segmentation first.

The type of growth that I have described for *Capsulata edenensis* n.gen., n.sp. is rare, at least among cyclophyllidean tapeworms. It does not involve schizogenesis or the production of secondary individuals as in some of the other species mentioned earlier, nor is a pseudoscolex formed. The anterior segmentation may however play a part with the rather small scolex in assisting the worm to remain in position in the gut of the host as many of the worms were found unattached in the intestine. It is difficult to account for this almost unique type of growth encountered in this species. It is possible that this type of growth is not as rare as its absence from the literature might suggest, and it may be worth while investigating other species in the same way. It is however unfortunate that it is not often that one finds enough material, with different stages of growth, and also in a good enough state of preservation to enable an investigation of this type to be carried out.

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A New Technique for the Recovery of Infective Strongyle Larvae from Soil and Pasture

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In studies on parasitic gastro-enteritis of cattle which have been in progress at the Veterinary Parasitology Laboratory, Yeerongpilly, for a number of years, attention is being given to conditions which influence the development, distribution, and survival of the preparasitic stages of the various species of strongyles in the pasture. This has involved an exploration of methods for the recovery of infective larvae from soil and pasture.

Several techniques have been recorded by various workers for isolating nematode larvae from the different types of medium in which they live. The best known and most widely used is the Baermann technique, a detailed description of which is given by Cort *et al.* (1922). This technique and various modifications of it have been critically tested by a number of workers, including Kauzal (1940), and Dinaburg (1942), and there is general agreement that with both the original method, and also with the modifications, the percentage recovery of larvae is very variable, and frequently very low. Other techniques include that of Roberts and O'Sullivan (1950) for the recovery of larvae from cattle faecal cultures, and that of Beaver (1953) for the isolation of hook-worm larvae from soil. All of these techniques rely on the active migration of the larvae from the medium, under a stimulus provided by temperature, moisture, light, and gravity.

The writer's observations, based on a number of tests, indicate that, at least with the infective larvae of the cattle strongyles, these techniques fail because many larvae, after an initial phase of activity, become motionless for long periods when they assume a characteristically coiled form. The technique developed by Roberts and O'Sullivan (1950), for example, can be depended upon to give a high recovery of larvae from faecal cultures, but is quite unsuitable for soil and pasture samples. Attention has therefore been directed towards a method in which the larvae were given a wholly, or partially passive role. The most satisfactory of these is described below.

DESCRIPTION OF APPARATUS

The technique relies on the difference in density of larvae and debris under the influence of a stream of water flowing upwards at a gradually decreasing flow rate.* The overflow from the apparatus carries the larvae with it, and is passed through a stainless steel sieve of 23μ aperture in which they are trapped.

The apparatus is illustrated in Fig. 1. It consists of a glass funnel (c) 10 in. in diameter, suspended by three wires attached through holes bored in the glass, approximately $\frac{1}{2}$ in. below the rim. The length of each wire is adjusted independently by a small turn-buckle (a) placed within its length to keep the rim of the funnel level. A conical trap (d) to collect water flowing over the rim is fitted around the outside of the stem of the funnel with a rubber stopper (f). A water inlet tube (h, j, k) consisting of three 4 in. pieces of 1 in., $\frac{1}{2}$ in., and $\frac{1}{4}$ in. O.D. glass tubing, joined together, is attached to the stem of the funnel by means of a short piece of rubber tubing [Fig. 1 (g)]. It is not considered that these dimensions of the water inlet tubes are critical, so long as the tubing is sufficiently long, and gradually increasing in diameter to promote an upward flow of water which decreases slowly in flow rate.

The trap [Fig. 1 (d)] is fitted with an outlet from which a piece of rubber tubing leads into a conical stainless steel sieve** with a mesh aperture of 23μ .

The sieve is conical in shape, with a height of 7 in., and a rim diameter of 5 in. It is strengthened by three stainless steel rods [Fig. 1(b)] on the outside extending from the rim to the apex. The rim of the sieve is supported by a strip of stainless steel [Fig. 1(o)] approximately 1 in. in width. The apex of the cone is open and is soldered to a piece of $\frac{1}{2}$ in. stainless steel tubing [Fig. 1(q)] approximately $1\frac{1}{2}$ in. long. The outlet of the funnel so formed is closed with a piece of rubber tubing fitted with a burette clip.

*Since these investigations were completed, the writer has read of a technique developed by Seinhorst (Goodey 1957) for the recovery of nematodes from soil, which is also based on the separation of nematodes from inert particles by using a slow, upwardly directed current of water. Although a high recovery is claimed, the method seems too cumbersome for the routine recovery of parasitic strongyle larvae from soil and pasture, both because of the complicated procedure and the time involved.

**The sieve was constructed from stainless steel micro-straining fabric MKO, supplied by Glenfield and Kennedy Ltd., 105 Park Street, London W.1.

PROCEDURE

(a) Treatment of Pasture Samples.—A pasture sample of approximately one pound weight is covered with water to which 1 ml. of an anionic detergent has been added to facilitate the wetting of the sample and of the larvae, thus rendering the washing process more efficient. A non-ionic detergent may have similar effects as observed by Rohrbacher (1957). After standing for two

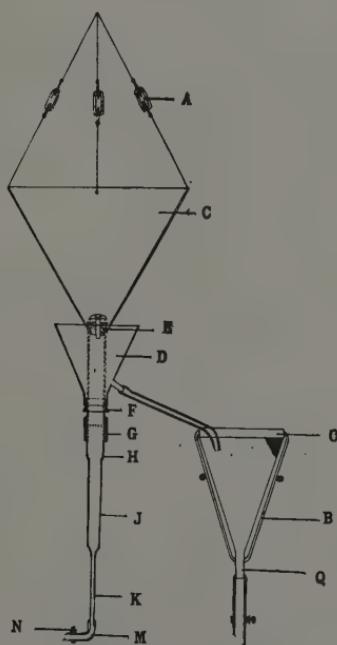


Fig. 1

to three hours to allow larvae to become detached, the pasture sample is washed thoroughly in three changes of water, using approximately one gallon of water for each washing. The washings are passed through a sieve of 40 meshes to the inch, and allowed to stand for six to eight hours, or preferably overnight. The supernatant is then removed with a water suction pump, leaving the sediment in which the larvae are present.

(b) Treatment of Soil Samples.—The apparatus will treat a soil sample weighing up to 50 g. The soil is broken up in water, using a mechanical stirrer, until the larger aggregations have disintegrated. The suspension is passed through a 40 mesh sieve, and the sieve is washed thoroughly with a fine jet of water. The washings from the sieve contain soil particles and larvae.

(c) Separation of Larvae.—The soil or pasture sediment is treated with a saturated solution of iodine in potassium iodide, to kill the larvae, as it has been found that the sieve is more efficient in retaining dead larvae than living ones.

The sediment is poured into the funnel and allowed to settle for one or two minutes. When samples with large amounts of sediment are being treated, the sediment tends to collect around the inlet to the funnel and, consequently, is not washed satisfactorily. To overcome this difficulty, a cork fitted with a double "T" piece [Fig. 1 (e)] of $\frac{1}{4}$ in. glass tubing, with outlets in the form of a cross, is inserted into the inlet of the funnel.

Water is then allowed to flow slowly into the funnel from a constant-head reservoir, the rate of flow being determined by adjusting the burette clip [Fig. 1(n)]. When the funnel commences to overflow, it is levelled by means of the turn-buckles to give an even flow of water over the rim. The overflow is collected in the conical trap and passes into the sieve. The flow rate may then be adjusted so that the sediment is subjected to gentle agitation by allowing a flow at the rate of 600 to 800 ml. per minute. If the volume of water flowing through the apparatus is much less than 600 ml. per minute, larvae will not be carried out with the overflow, whereas if the flow rate is too great, too much debris is carried out with the overflow. The apparatus is allowed to run for one hour.

If the sieve tends to become blocked during the procedure, it may be cleared by directing a jet of water onto the inside surface. When the washing has been completed, the sieve is allowed to drain for some minutes to reduce the residual water to a minimum.

The burette clip which seals the end of the sieve is opened and contents are run into a 100 ml. measuring cylinder. The sediment and larvae remaining in the sieve are washed out with approximately 50 ml. of water directed at the inner surface of the sieve as a fine jet. The total sediment is then made up to 100 ml. in the measuring cylinder. Aliquots of 1 ml. are taken after thorough mixing of the sample, and the larvae are counted in the counting chamber shown in Fig. 2.

To empty the apparatus, the double "T" piece is removed and the tube [Fig. 1(m)] detached from the apparatus, which allows the sediment and water remaining in the funnel to be discarded. The apparatus may then be washed out with a stream of water, and is ready for the next sample. There is no need to dismantle the apparatus between samples.

THE COUNTING CHAMBER

The examination of the 1 ml. aliquot is simplified by the use of the glass counting chamber shown in Fig. 2.

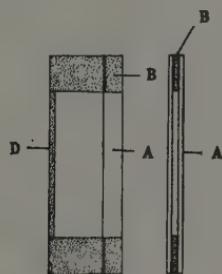


Fig. 2

The chamber consists of a 3 by 1 in. glass microscope slide [Fig. 2(a)] forming the base, with pieces of glass of similar thickness, and 1 in. by $\frac{1}{2}$ in. in size superimposed, on each end [Fig. 2(b)]. The rear edge of the slide is sealed with a strip of glass [Fig. 2(d)] $\frac{1}{8}$ in. in width, and of the same thickness as the end pieces, so that a platform is formed around three sides of the base. Another glass slide 3 by $\frac{3}{4}$ in. is fixed on top of the platform so that a shallow chamber 2 by $\frac{3}{4}$ by $\frac{1}{8}$ in. is formed, into which the 1 ml. aliquot is introduced. The volume of the chamber is slightly in excess of 1 ml.

The parts of the counting chamber are sealed together with the glass cement described by Whitlock (1948). Its dimensions may be varied according to the volume of fluid to be examined, and also to suit the width of traverse of the particular type of mechanical stage used. The chamber is useful for counting larvae for any purpose. Its capacity should be such as to permit the addition of iodine solution, when live larvae are being counted.

This type of slide may be handled without spillage if reasonable care is taken, and larvae can be counted accurately right up to the edge of the chamber. There is little necessity to alter the focus of the microscope during examination as the liquid is of the same thickness throughout. The chamber is easy to clean and may be washed out with a jet of water.

EFFICIENCY OF TECHNIQUE

The technique has been tested for the recovery of larvae from both pasture sediment and soil samples, into which known numbers were introduced. Larvae were introduced into the sediment obtained by washing uncontaminated pasture samples, since it is impossible to reproduce artificially the distribution of larvae on pasture, as they would be in samples collected from the field.

A mixture of infective larvae of the following cattle strongyles was used : *Haemonchus placei* (Place 1893), *Trichostrongylus* sp., *Cooperia* spp., *Ostertagia* spp., and *Oesophagostomum radiatum* (Rud. 1803). Larvae of *H. placei* and *Cooperia* spp. predominated. The results of these test recoveries are given in Table 1.

The recovery from pasture samples ranged from 61 to 94%, with an average of 74%, and from soil samples between 55 and 94%, with an average of 78%.

An analysis of the tests in Table 1 shows that there is no significant difference in the larval recoveries from soil and pasture sediment samples, either in the average values, or in the standard errors. On grouping the data, an average recovery rate of $76\% \pm 10\%$ was calculated.

These recovery rates were obtained by running the apparatus for one hour. It is reasonable to assume that by increasing this period, a greater recovery of larvae should be obtained. Furthermore, the total number of larvae recovered by the technique was estimated by counting only three 1 ml. aliquots from a total volume of 100 ml. It is obvious that the greater the number of aliquot samples counted, the more accurate would be the estimate of the total number of larvae in the sample. However, when large numbers of samples have to be handled, any such possible increase in accuracy would not warrant the extra labour involved.

The technique has proved quite satisfactory for measuring the changes that occur in larval populations in the field, and has been found useful for recovering immature trichostrongyles from intestinal contents.

TABLE 1

The recovery of larvae after known numbers had been introduced into uncontaminated soil and pasture sediment samples

Sample No.	Type of Sample	No. of Larvae Introduced	No. of Larvae Recovered	% Recovery
1	Pasture	1,289	867	67
2	"	776	600	77
3	"	400	300	75
4	"	241	167	69
5	"	598	367	61
6	"	173	133	77
7	"	354	333	94
8	"	447	333	74
9	"	438	333	76
10	Soil	650	533	82
11	"	227	200	88
12	"	424	400	94
13	"	225	200	89
14	"	350	233	67
15	"	182	133	73
16	"	175	133	76
17	"	183	100	55
18	"	732	633	86
19	"	100	67	67
20	"	394	300	76

ACKNOWLEDGMENTS

The author wishes to thank Mr. K. E. Dixon, who carried out a large portion of the trials involved in testing the technique, and Dr. F. H. S. Roberts, D.Sc., Officer-in-Charge of the Veterinary Parasitology Laboratory, C.S.I.R.O., Yeerongpilly, for his helpful advice and criticism during the course of this work.

SUMMARY

A new technique for the recovery of Trichostrongyle larvae from soil and pasture samples is described.

The technique is based on the difference in density of larvae and debris under the influence of a stream of water flowing upwards at a gradually decreasing flow rate.

The results from trials with known numbers of larvae gave an average recovery of 74% from pasture, and of 78% from soil.

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Studies on Digestion in the Monogenetic Trematode *Polystoma integerrimum*

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Previous accounts of *Polystoma integerrimum* have been confined almost entirely to descriptions of the anatomy and life history and little is known of its physiology and in particular of its nutrition. Gallien (1934) concluded from the red colour of the gut contents that both the adult stage in the frog bladder and the neotenic and larval stages on the tadpole gill feed upon blood, and suggested that the dark insoluble pigment and various crystals which occur in the gut cells (Zeller, 1872, 1876) are probably end products of digestion. The pigment was identified as haematin—a degradation product of haemoglobin—by Llewellyn (1954) and this further indication that *Polystoma* feeds on blood was confirmed by Jennings (1956) who showed also that haematin is periodically voided by the parasite and can be detected in the urine of an infected frog. The nature of the crystals and the details of digestion remained unknown but the occurrence of both crystals and haematin within the gut cells suggested that breakdown of blood in *Polystoma* is either partially or entirely intracellular. The present investigation was undertaken to clarify this point and to make available a general account of digestion in the adult stage of this trematode.

MATERIAL AND METHODS

Specimens of *Polystoma* were obtained from infected frogs detected by examination of the urine for haematin (Jennings, 1956) and those judged to be newly fed from the bright red colour of their gut contents were isolated in frog Ringer and fixed at progressive intervals for histological examination. It was found that a larger proportion of such newly fed individuals could be obtained if infected frogs were pithed and left for thirty minutes before removal of the parasite, indicating that the fall in blood pressure and muscular relaxation after death in some way facilitates feeding. Fixation was in warm 10% neutral formalin, a neutral fixative being necessary

to preserve the acid soluble crystals of the gut, and sections cut at 8μ were stained by haematoxylin and eosin, Feulgen and the benzidine peroxide method for haemoglobin. The gut crystals were tested for their reactions to methylene blue, the Prussian and Turnbull's blue methods for iron and Gmelin's test for bile pigments as modified for histological use by Pearse (1953).

OBSERVATIONS

The structure of the gut.

The pharynx opens into the bifid gut whose caeca run the length of the body and give off branches which repeatedly subdivide and anastomose. Microscopically the gastrodermis consists of columnar cells, $16-18\mu$ tall when mature, with large vesicular nuclei, and standing on a well-defined basement membrane (Plate 1A). They contain varying amounts of haematin, depending upon the stage reached in the digestion of the most recent meal. Thus there may be only a few fine granules scattered through the cytoplasm but if the *Polystoma* has only recently fed the cells may be so loaded with pigment that the nucleus and other details are obscured. The granules of haematin are occasionally uniformly distributed through the cytoplasm but usually they are confined in spherical aggregations $5-10\mu$ in diameter and bounded by a definite membrane (Plates 1A and C). Fixation often causes the granules to clump into solid masses but in life they are free from each other and in constant Brownian movement within the confining membrane. The spheres and haematin particles are eventually extruded from the cells (Plate 1A) into the gut lumen where the former disintegrate and liberate their contents. Extrusion of the spheres is followed by shrinkage of the cells and often this is so great that only the nucleus and a little cytoplasm is left. All stages have been seen between such shrunken cells and large mature cells loaded with haematin, and it is clear that once a cell has discharged its spheres it grows and forms more haematin so that the gastrodermis is constantly renewed. Occasionally entire gut cells break down either *in situ* or after moving into the lumen, having apparently lost the capacity for further regeneration, and if many such spent cells disintegrate at the same time large areas of the gut wall become completely denuded of cells and only the basement membrane persists. It is not known how these spent cells are replaced, but it is probable that the surrounding gastrodermis gradually extends inwards to cover the denuded area.

The crystals described by Zeller and Gallien occur in only 5–10% of the gut cells, in contrast to the almost ubiquitous distribution of haematin. Like the latter they are only formed intracellularly but with growth come to protrude from the cell and are finally expelled into the lumen (Plate 1C). Only one crystal is formed per cell and usually the formative cell contains little or no haematin. They are needle-like or rhomboidal in shape, reaching 15–25 μ in length, and vary from a yellowish green to colourless. These features are best seen in fresh squashes as the crystals are acid soluble and even a neutral fixative may cause distortion and partial solution. The crystals give negative results to tests for haemoglobin and ferrous or ferric iron but stain strongly with methylene blue, and this combination of properties in a substance formed in circumstances indicating it to be a product of blood digestion suggested that it was haematoidin—an iron-free degradation product of haemoglobin chemically identical with vertebrate bilirubin. This identification was confirmed when the crystals gave a positive reaction to the modified Gmelin test which, according to Pearse (1953), is completely diagnostic for haematoidin and bilirubin.

The course of digestion

The formation within the gut cells of both haematin and haematoidin shows that there is a considerable amount of intracellular digestion of haemoglobin in *Polystoma* but there is no evidence that the cells are phagocytic. Thus the intracellular process must be preceded by some intraluminal breakdown with subsequent absorption of semi-digested products and this was confirmed when individuals fixed at progressive intervals after feeding were examined.

Sections of *Polystoma* containing bright red newly ingested blood showed the gut to be filled with a mass of haemolysed erythrocytes staining heavily with benzidine. Very few intact erythrocytes were ever found, although many newly fed individuals were examined, so that haemolysis must occur during or immediately after ingestion. The erythrocyte nuclei, however, remain intact and stain strongly with Feulgen (Plate 1B) and are scattered throughout the haemolysed mass along with free granules of haematin and occasional crystals of haematoidin. The gastrodermis at this stage is quite normal, with occasional cells discharging spheres of haematin or crystals of haematoidin, but there are no signs of extracellular secretion of digestive juices.

Two to three hours after feeding few intact erythrocyte nuclei remain, but the entire mass in the gut lumen now stains lightly with Feulgen indicating that the contents of the disintegrated nuclei have become mixed with the rest of the food. The Feulgen reaction decreases with time, the digesting food starting to take the green counterstain, and six hours after feeding no material staining with Feulgen can be found in the lumen. Exactly parallel conditions are seen in sections stained with benzidine, the haemoglobin of the haemolysed erythrocytes having mixed with the rest of the gut contents, causing them to stain a uniform and intense blue until about three hours after feeding. The reaction then gradually disappears and after a further three hours very little unchanged haemoglobin is left.

This intraluminal digestive activity during the first six hours after feeding is accompanied by active absorption of semi-digested materials by the gastrodermis, the cells becoming swollen with absorbed substances showing the same staining reactions as those remaining in the lumen. Thus three hours after feeding, the gut cells are distended with absorbed material which stains with Feulgen and is either uniformly distributed about the cell or concentrated in well defined masses quite distinct from the rest of the cytoplasm (Plate 1D). Staining with benzidine gives similar results, with unchanged or partially digested haemoglobin absorbed by the gut cells showing a decreasing reaction as intracellular digestion progresses. Six hours after feeding the gut cells are still swollen but their contents, like those of the lumen, no longer give specific staining reactions. As absorption by the gut cells progresses the material in the lumen decreases rapidly in volume and twelve hours after ingestion very little remains.

At about this point the amount of haematin and haematoidin in the gut cells, which has so far remained constant, starts to increase and at eighteen hours the cells are loaded with these substances. The haematin appears either scattered through the cytoplasm or in the characteristic spherical aggregations (Plates IA and C), and these latter are clearly derived from the intracellular concentrations of absorbed material seen three hours after feeding (Plate 1D). The loaded cells occasionally disintegrate but the majority extrude their contents, with consequent reduction in size, and now for the first time since digestion began there is a significant increase in the amount of haematin and haematoidin in the lumen. Thus the final degradation of haemoglobin into these substances must be confined

to the gut cells, since the lumen is almost empty twelve hours after feeding and the amount of intraluminar pigment and crystals does not increase for another six hours. Haematin and haematoidin accumulate in the lumen and are periodically voided through the mouth, but evacuation of the gut is never complete, owing to its diffuse nature, and it always contains small amounts of these substances.

Thirty-six hours after feeding, the gastrodermis has returned to normal, with some of the cells discharged and reduced in size but ready to enlarge as soon as more material is available for absorption during digestion of the next meal. Other cells retain varying amounts of haematin and haematoidin and the gastrodermis is never at any time completely free of them, some persisting even in *Polystoma* kept in frog Ringer for ten days after feeding which is the maximum period the flatworm would survive after removal from its host.

DISCUSSION

It is evident from these results that digestion in the adult *Polystoma* is the result of both intraluminar and intracellular processes; the latter occurring after absorption of partially digested material from the lumen and achieving the final stages in the breakdown of haemoglobin into haematin and haematoidin. No specific source of the enzymes responsible for intraluminar digestion has been found but since the spherical aggregations of haematin extruded from the gut cells arise as sites of intense intracellular digestive activity it is probable that enzymes persist in them and are released in the lumen when the spheres disintegrate. The incomplete evacuation of the gut and the fact that extrusion of spheres continues, to a small extent, between meals both ensure that the gut is never completely cleared and released enzymes could persist and mix with newly ingested blood to effect haemolysis and partial digestion. Thus intraluminar digestion in *Polystoma* appears to be an incidental extension of the primitive intracellular method, arising as a consequence of the blood feeding habit and the resultant need to eliminate unwanted and insoluble products of haemoglobin degradation from the gut cells. An exactly parallel digestive process has been described in the lamellibranch *Lasaea rubra* (Morton, 1956) where cells of the digestive gland discharge spheres which fragment to release unwanted residues and, it is believed, the enzymes responsible for intraluminar digestion.

Llewellyn (1954) believed the gut cells in *Polystoma* and related trematodes to be phagocytic but no evidence in support has been found here. In the early stages of digestion abundant intact erythrocyte nuclei are available for phagocytosis but they are never seen within the gut cells. Food enters the gastrodermis from the lumen by absorption only, after first being rendered soluble, and this has the advantage that the insoluble haematin and haematoidin are barred from re-entering the gut cells which might occur if these were phagocytic. Phagocytosis in the flat-worms is often totally unselective (Jennings, 1957) and if such occurred in *Polystoma* there would be great difficulty in eliminating the end products of digestion.

The normal adult *Polystoma* produces only a small amount of haematoidin crystals but its neotenic form, which becomes sexually mature whilst still in the larval habitat on the tadpole gill, is reported to form very much more (Gallien, 1935; Williams, 1958) and this may well reflect a fundamental difference in nutrition and digestion from which stem all other differences between the two forms.

End products of digestion similar to those formed by *Polystoma* have been reported in a variety of other parasites which feed upon vertebrate blood. Bile pigments and haematin have been described in the gut of the bug *Rhodnius* and the louse *Pediculus* (Wigglesworth, 1943), and in the peritoneal cells of the leech (Speiss, 1905), whilst haematin alone is produced by species of *Plasmodium*. Amongst the trematodes haematin formation has been described in *Schistosoma* (Rogers, 1940), *Fasciola* (Stephenson, 1947), and various Monogenea (Llewellyn, 1954), and digestion in these flatworms is probably essentially similar to that in *Polystoma*. Formation of haematin is not, however, common to all blood-feeding trematodes for *Haplometra* and *Gorgodera* are often found with blood in the gut but with no trace of this pigment, so that digestion in these forms must follow some alternative course to that described here.

SUMMARY

1. The adult stage of *Polystoma integerrimum* feeds on blood which is digested by a combination of intraluminal and intracellular processes, haemolysis and partial digestion in the gut lumen being

followed by absorption and completion of digestion by the cells of the gastrodermis.

2. The end products of intracellular digestion are the pigment haematin and a crystalline substance identified as haematoidin, which is chemically identical with vertebrate bilirubin, and these are passed back into the lumen to be eventually voided to the exterior.

3. It is probable that the expulsion of haematin from the gut cells results in a simultaneous release of enzymes, traces of which persist in the lumen to effect the early extracellular stages in the digestion of the next meal, so that intraluminal digestion in *Polystoma* appears to be an incidental extension of the primitive intracellular process arising from the blood-feeding habit and the consequent need to eliminate residues of haemoglobin breakdown from the gastrodermis.

4. Since haematin formation has been described in certain other trematodes it is suggested that their digestive processes probably follow a course similar to that described for *Polystoma* but an alternative method must exist within the class since other blood feeders such as *Haplometra* and *Gorgodera* do not form this pigment.

ACKNOWLEDGMENTS

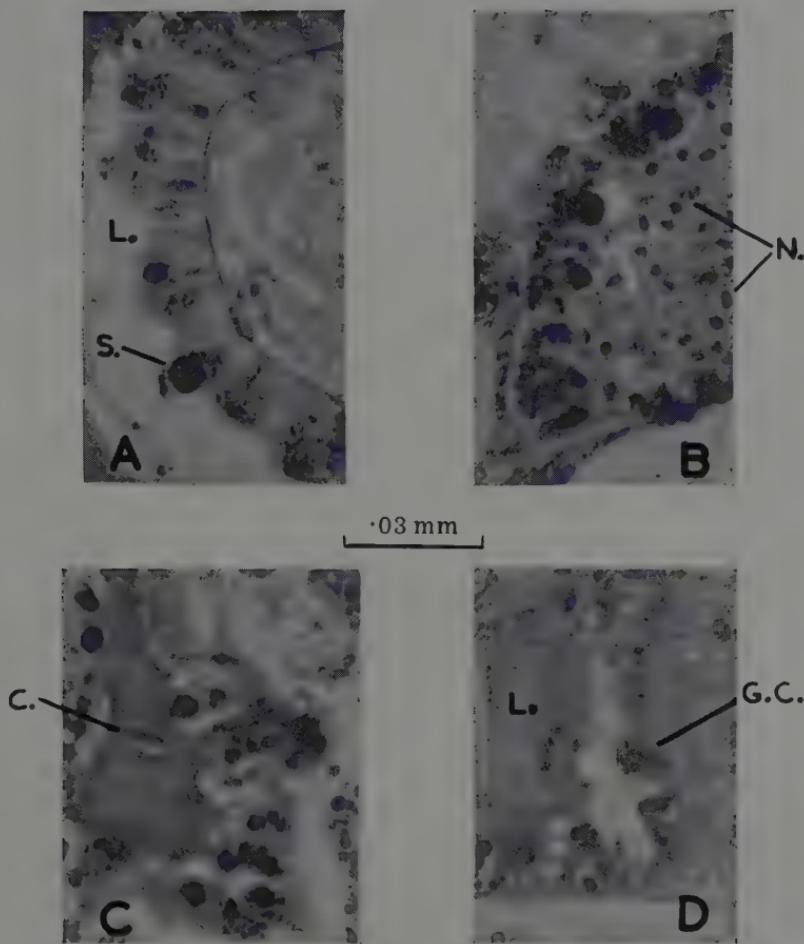
I am grateful to Professor E. A. Spaul and Dr. T. Kerr for their advice and kindness in reading and criticising the text.

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PLATE I



1.—*Polystoma*. Section of the gastrodermis showing a sphere (S.) packed with haematin granules being extruded into the gut lumen (L.). Haematoxylin and eosin. B.—*Polystoma*. Section of the gut immediately after feeding, with haemolysed corpuscles and intact erythrocyte nuclei (N.) in the lumen. Feulgen and Fast Green. C.—*Polystoma*. Section of the gut showing a crystal of haematoxylin (C.) lying free in the lumen. Haematoxylin and eosin. D.—*Polystoma*. Section of the gut three hours after feeding showing complete breakdown of erythrocyte nuclei in the lumen (L.) and a concentration of absorbed material in the gut cell (G.C.). Feulgen and Fast Green.

Abnormal Migration in *Polystoma integerrimum*

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Rana temporaria tadpoles which had been naturally infected by larvae of *Polystoma integerrimum* were kept in the laboratory under conditions precluding the continuous re-infection which occurs in nature. One tadpole was seen to have two larvae attached to the skin of the ventral surface of the body, which were moving towards the posterior end. The tadpole measured 7.9 mm. in body length and 20.8 mm. in total length, and its stage of development corresponded to stage 5 in the table of development and metamorphosis compiled by Rugh (1951); it was collected in mid-May and had been kept for twelve days under laboratory conditions. The tadpole was fixed and dissected: the bladder had not developed, and the gills showed no indication of atrophy; the alimentary canal was long and heavily coiled, and filled with food. In addition to the two larvae observed on the skin, one larva was found in the branchial chamber, two were in the cloacal tube, seven occupied the cloacal chamber and two had travelled up the right ureter to the kidney; the alimentary canal was free of larvae. All fourteen larvae were gyrodactyloids.

The larvae parasitizing this tadpole had evidently undergone migration prematurely in response to an abnormal stimulus. Normally, the radical re-organization of the alimentary canal which occurs at metamorphosis enables the parasites to migrate internally through the length of the gut to the cloacal chamber and thence to the newly-formed bladder; this re-organization entails shortening and straightening of the alimentary canal and a period of starvation during which it is emptied. In this exceptional case, however, the migration of the parasites was not synchronized with the metamorphic changes in the alimentary canal and internal migration was impossible. It is of interest that the parasites, having a life history finely adjusted to that of the host, should nevertheless be capable of this abnormal mode of migration.

The nature of the stimulus influencing the larvae to migrate is unknown. It has been suggested that atrophy of the gills provides the stimulus for migration; however in the present case the gills of the tadpole had not undergone reduction.

Because the larvae had migrated prematurely, the bladder was undeveloped when they reached the cloacal chamber; presumably they could not have survived had metamorphosis not taken place soon afterwards. The discovery of two of the specimens in the ureter suggests that the larval worms may be chemically attracted to urine.

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Preliminary Note on the Anatomy of a Polystome from the Bladder of *Xenopus laevis* Daud.

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Six specimens of *Xenopus laevis* obtained from University College, London, were examined for polystomes; one harboured an adult worm measuring 2·1 mm. in length and two immature specimens, both 0·8 mm. in length, and one was parasitized by a single mature specimen measuring 2·4 mm. in length.

The parasites possess a caudal disc bearing a single pair of large anchors with bifurcated shafts and six suckers resembling those of *Polystoma*.

The heavily branching intestinal crura unite posteriorly and are joined by a number of transverse branches. Anastomoses between the crura are already established in the immature specimens.

A penial coronet, comprising eight large spines and eight smaller spines, surrounds the terminal portion of the male duct. The large and small spines are set alternately. Vaginae are completely absent.

Gland cells of two kinds occur in association with the ootype as in *Polystoma integerrimum*, Fröhl., (Williams, 1957). The ducts follow the same course in both species. There is no uterus.

This African species resembles the neotenic adult of *P. integerrimum* in having neither uterus nor vaginae; in both these forms insemination can only take place through the short ovo-vitelline duct.

The species is provisionally identified with *Polystoma xenopi* Price, 1943, which was placed in a new genus and renamed *Protopolystoma xenopi* by Bychovsky, 1957. The form described by Price parasitized *Xenopus laevis* and evidently possessed neither uterus nor vaginae.

However, the description given by Price fails to correspond with the present form in that the intestinal crura are stated to be unconnected posteriorly and to lack transverse anastomoses. Also, that author mentions no inequality in the size of the penial coronet; the number of spines is given as approximately fourteen.

Protopolystoma, while having the location within the host characteristic of the normal form of *Polystoma*, has fundamentally the same structure as the neotenic adult of this genus. *Protopolystoma* may be a neotenic form, rather than primitively simple in structure. The occurrence of a uterus in polystome genera parasitizing terrestrial amphibia is probably related to the need to produce large numbers of eggs during the host's brief visit to the ponds during the breeding season. The uterus, which forms late in the development of the normal form of *Polystoma*, may have been lost in *Protopolystoma* as a result of neotenic development in correlation with the adoption of a permanently aquatic mode of life by the host.

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On *Cercaria owreae* (Hutton, 1954) from *Sagitta hexaptera* (d'Orbigny) in the Caribbean Plankton

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Many observations have been made of the occurrence of larval Digenea in planktonic animals. These are originally free forms in the plankton which later penetrate or are eaten by pelagic coelenterates, copepods and chaetognaths. Best known are members of the genera *Hemimuris* and *Derogenes* (Hemimuridae) and *Opechona* (Allocreadiidae). Dollfus *et al* (1954) named a score of writers who have observed such parasites in *Sagitta*, sometimes without leaving adequate records, and also described from *S. enflata* near Madras tailless and unnamed Accacoeliidae which are possibly a species of *Tetrochetus*. Members of this family when adults are mainly parasites of the sunfish *Mola mola* (L.). The forms to be described are also in all probability Accacoeliids, belonging however to a different genus. Hitherto they have been seen once only and Hutton (1954) named them *Metacercaria owreae*. In reality they are cercariae and are now given the appropriate name *Cercaria owreae*. They represent a new type of distome cercaria for which the name "Diplocercous" is now proposed.

MATERIAL

Various species of *Sagitta* collected during the cruise of Lord Moyne's yacht "Rosaura" (1937-38) were recently examined by John S. Colman, who kindly gave the writer the parasitised specimens. They are all *S. hexaptera* and were all collected in four Caribbean localities.

Lot	Station and Locality	Number of hosts examined	Number parasitised	Number and designation of the parasites
1	15 (between Cuba and Jamaica)	43	3 (A, B, C)	4 (Aa, Ba, Ca, Cb)
2	27 (off Roatan Island) ...	51	2 (A, B)	4 (Aa+, Ab+, Ba, Bb)
3	32 (250 miles NNW of Colon)	63	6 (A—E)	6 (Aa, Ba, Ca+, Da, Ea, Fa)
4	33 (off Puerto Columbia)	13	1 (A)	1 (Aa+)

(A plus sign denotes parasite retained *in situ*)

In addition, two *S. hexaptera* collected at Station 14 (Tongue of Ocean, Bahamas) and nine collected at Station 28 (N. of Bonacca Island) did not contain any parasites. Thus, 181 *S. hexaptera* were from the Caribbean and 12 of them provided a total of 15 trematodes. Another 109 *S. hexaptera* collected elsewhere were also free of parasites; 44 from Station 42 (off N.E. Brazil), 25 from Station 43 (off E. Brazil), 27 from Station 45 (N. edge of N. Equatorial Current) and 13 from Station 46 (Guinea Current). Parasites were not found either in 141 *S. enflata*, 110 *S. lyra* and 167 *S. maxima* collected in various localities. Details regarding Stations are given in Colman's paper (1954). Three of the parasitised *S. hexaptera* contained two parasites, the remaining nine one each.

METHODS

The hosts were fixed in formalin at sea but later transferred to alcohol. They were stained in borax carmine, differentiated, dehydrated, cleared in cedar-wood oil and promptly dissected. The host's tissues were cut with needles and the larvae extracted untouched by means of a fine pipette, transferred to fresh oil and mounted in Canada balsam. These conventional methods produced presentable mounts. Four larvae kept *in situ* in three hosts prove that the location is the coelom as well as the gut, and the fleshiness of the body in large specimens is more obvious in such mounts. Drawings and measurements are based on camera lucida drawings. All measurements were made thrice, without using any particular order, and close conformity was obtained. Three specimens were sectioned serially at 10 μ , one frontally and the others transversely. Valuable information regarding the structure of the cuticle, the caeca and their diverticula, the stalk and the appendages was

gained from the sections. Several specimens were photographed, and some such evidence has been published already in a preliminary note (Dawes, 1958).

DIAGNOSIS

Body ovoid, 0·28–1·20 mm. long and 0·17–0·75 mm. in greatest breadth. Cuticle thick, finely granular and delicately furrowed. Oral sucker sub-terminal, 0·06–0·24 mm. diameter, ventral sucker centred in the anterior region, 0·12–0·37 mm. diameter. Prepharynx absent, pharynx present, oesophagus directed forward, bifurcation of gut T-shaped, caeca sacculated. Anterior end of each caecum having a rosette of six small diverticula. Excretory pore transversely elongate, excretory canals Y-shaped, much folded. Genital pore median, situated between the suckers, gonads extremely rudimentary. Two posterior appendages present, length extremely variable (0·11–1·24 mm. long) and not proportionate to body-length, breadth 0·04–0·14 mm. Each appendage attached to the body by a narrow stalk passing through the excretory pore to the wall of the excretory vesicle and containing an extension of the caecum of the same side. Cuticle of the appendages very thin, remaining tissue mainly muscle cells with some parenchyma. Parasites in the intestine and body cavity of *Sagitta hexaptera* collected in the Caribbean Sea.

DESCRIPTION

Size and shape. The shape is ovoid and broader posteriorly (Fig. 1) and small specimens are delicate and translucent, larger ones fleshy and opaque. The two largest specimens (14 and 15) seem to be transitional forms between larva and juvenile with a more cylindrical body and deeper superficial furrows, particularly in the posterior region, where they are concentric around the sub-ventral excretory pore. Specimen 14 has small and somewhat shrunken appendages, specimen 15 no appendages.

The smallest specimen measures 0·28×0·17 mm. and the largest 1·20×0·75 mm. Over the entire size range breadth is 61–76% of body-length, excepting the extended specimen 8 in which it is 54%.

Nine specimens are less than 0·5 mm. long; their mean length is 0·38 mm. and mean breadth 0·25 mm. (=64% body-length). The remaining six specimens have a mean length of 0·84 mm. and their mean breadth is 0·54 mm. (=0·64% body-length). Breadth may therefore be taken as fairly constant and about three-fifths of body-length. The region of the body posterior to the ventral sucker increases in relative length, however, from 29 to 57% body-length. (Table 2, Column E). About three-tenths of the body is post-acetabular in small specimens, nearly three-fifths in larger ones. This extension of the posterior region can be seen by inspection (cf. A and D, Fig. 1) and it is the beginning of a trend that will continue during post-larval life.

Oral sucker. The diameter of the oral sucker is about 0·06–0·24 mm. (=17–25% body-length) (Tables 1 and 2). In five of the smallest specimens the diameter is 21–25% body-length (mean 24), in five of intermediate size it is 19–21% (mean 20), and in five of largest size it is 17–21 (mean 20). The mean diameter of the sucker for all the specimens is 0·12 mm. (=21% body-length). It is approximately true to state therefore that the diameter of the oral sucker is about one quarter of body-length in small specimens and one-fifth in larger ones. This sucker is however relatively very deep (see Fig. 1E) and this is a dimension which could not be measured.

Ventral sucker. This sucker is generally transversely oval in outline and situated immediately behind the oral sucker, a deep fold intervening. The length ranges from 0·12 mm. to 0·37 mm. (=43–22% body-length) (Tables 1 and 2). In five of the smallest specimens the length of this sucker is 32–43% body-length (mean 36), in five of intermediate size it is 25–34% (mean 31), and in five of the largest specimens it is 22–31% (mean 29). If we relate the breadth of this sucker to the breadth of the body (0·17–0·75 mm.) for these three arbitrary groups of specimens, the corresponding percentages are 45–71 (mean 56), 39–61 (mean 52) and 40–52 (mean 48). Like the oral sucker, the ventral sucker diminishes slightly in relative size with increase in size of the body.

Cuticle. The cuticle is a dense layer 4–5 μ thick which stains deeply with haematoxylin. It is somewhat thinner in the cavities of the suckers, the pharynx and the excretory vesicle, and very thin on the appendages. Near the surface, numerous minute, deeply-staining granules are evenly spaced about their own diameter apart,

and where they occur the surface is slightly elevated. The surface is finely furrowed and in sections very slight obliquity reveals the overlapping edges of adjacent annulations, resembling the arrangement of tiles on a roof. At the free edges, where the section becomes

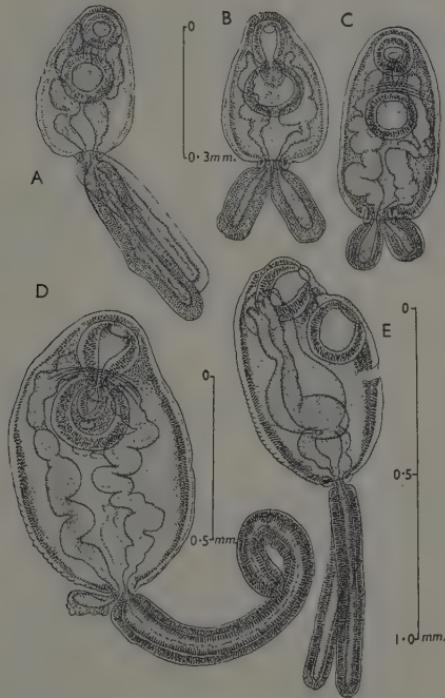


Fig. 1.—*Cercaria oureae*. A, B, C, D, and E representing specimens 4, 2, 8, 13 and 12 respectively. A—D from *Sagitta hexaptera* collected 250 miles N.N.W. of Colon. E, specimen kept *in situ* in the same host collected off W. end of Roatan Island.

very thin, the fine structure becomes more evident. Here can be seen regular arrays of the deep-staining granules both longitudinally and transversely, resembling the arrays of anisotropic regions in the sectioned myofibrils of striped muscle. Each annulus comprises 6 or 7 longitudinal rows of such granules and in tangential sections these are seen to be confined to the outermost region.

Table 1.—Measurements of body, suckers and appendages (mm.)

Specimen	Designation	Length of Body	Breadth of Body	Oral Sucker (dia.) l.x.b.	Ventral Sucker (size) l.x.b.	Appendages Length Breadth
1	2 Sta. 27Ab+	0.28	0.17	0.06-0.07	0.12 dia.	0.13 (2) 0.04
2	3 Sta. 32Ea	0.33	0.25	0.08	0.12×0.14	0.20 (2) 0.04
3	2 Sta. 27Ba	0.34	0.23	0.08	0.11×0.12	0.20 0.08
4	3 Sta. 32Ba	0.34	0.21	0.08	0.12×0.13	0.23 0.08
5	4 Sta. 33Aa+	0.40	0.29	0.10	0.13 dia.	0.44 0.09
6	1 Sta. 15Ba	0.41	0.27	0.08	0.13×0.15	0.20 0.08
7	1 Sta. 15Aa	0.41	0.29	0.08	0.14×0.16	0.23 Not seen
8	3 Sta. 32Da	0.43	0.23	0.09	0.14 dia.	0.11 0.09
9	3 Sta. 32Ca+S	0.49	0.31	0.11	0.17 dia.	0.12 0.08
10	3 Sta. 32Fa	0.52	0.33	0.09	0.13 dia.	0.32 (2) 0.09
11	1 Sta. 15Ca	0.67	0.45	0.13	0.16×0.18	0.48 0.10
12	2 Sta. 27Aa+	0.75	0.45	0.16	0.22 dia.	0.28 (1) 0.08
13	3 Sta. 32Aa	0.84	0.55	0.17	0.25 dia.	0.46 0.14
14	1 Sta. 15Cb	1.06	0.69	0.22	0.30×0.36	0.48 0.05
15	2 Sta. 27BBS	1.20	0.75	0.24	0.37 dia.	0.33 Not seen

Abbreviations : + = kept *in situ*. S = sectioned. (1), (2) number of appendages referred to ; if (1) one appendage only present.

Table 2.—Ratios of various dimensions ($\times 100$)

Specimen	(A)		(B)		(C)		(D)		(E)		(F)	
	Breadth of Body	Length of Body	Dia.	Oral Sucker	Length of Body	Sucker	Breadth Ventral	Sucker	Length Post.	Space	Length of Body	Length of Body
1	61	21-25			43		71		29		46 (2)	
2	76	24			36		66		36		61 (2)	
3	68	24			32		52		31		59 and 65	
4	62	24			35		62		38		123 and 129	
5	72	25			32		45		30		82 (2)	
6	66	20			32		56		35		49 and 56	
7	71	20			34		55		37		Not seen	
8	54	21			33		61		42		25 and 28	
9	63	22			35		55		35		65 (2)	
10	64	17			25		39		46		88 and 92	
11	67	19			22		40		52		42 (1)	
12	60	21			29		49		51		88 (2)	
13	65	20			30		45		55		147 (1)	
14	65	21			28		52		53		22 and 31	
15	63	20			31		49		57		Not seen	

Towards the posterior end of the body, where the furrows are deepened, the appearance of the cuticle is even more characteristic, scale-like flanges of it protruding, sometimes almost vertically. Folding of the cuticle gives this false impression of a scaly surface. The cuticular granules are not evidently of nuclear origin, being much smaller than the nuclei seen in any other tissues.

Muscle layers and parenchyma. Underneath the cuticle there are two layers of muscle fibrils, which can be seen in whole mounts and are strikingly evident in sections. The outer layer of circular fibrils is $6-8\mu$ thick, the inner layer of longitudinal fibrils about 4μ thick. Both layers are continuous throughout the body and not, as has been stated, confined to the posterior region. Between the two layers, conspicuous oval nuclei measuring about $2\mu \times 1\mu$ may be so crowded as to be only 5μ apart, or so sparse as to be more than 20μ apart. It is likely that these correspond to the outer muscle layer, because similar nuclei are seen underneath the inner muscle layer amidst those of the parenchyma, with which this layer makes delicate cytoplasmic connections separated by minute intervening spaces.

Underneath the muscle layers an outer zone of the parenchyma shows great density for a depth of about 25μ . This also can be seen in whole mounts. Sections show that most of this tissue consists of spindle-shaped cells with small nuclei, although the irregular inner edge of this zone is determined by very large cells measuring about $20\mu \times 15\mu$, more or less, with spherical nuclei about 6μ diameter. By their loose arrangement these large cells impart variable thickness to the dense outer zone of the parenchyma. Such cells as these have been accredited with the function of secreting and maintaining the cuticle, but indubitable connections with the cuticle were not seen in this trematode. The deeper parenchyma is much looser in texture and its spaces vary in size, being $10-80\mu \times 5-10\mu$ in extent. The more elongated spaces seem to be transversely arranged.

Alimentary canal. The mouth is not quite terminal. The pharynx abuts on the hind margin of the oral sucker, and may indent it slightly. The size of the pharynx is difficult to determine consistently,

the suckers generally obscuring this organ in whole mounts. It is however much smaller than the oral sucker and situated on the dorsal side of it, or a little farther back in the interval between it and the ventral sucker. The oesophagus extends forward dorsal to the pharynx and the bifurcation of the gut is to right and left immediately anterior to the pharynx. The two limbs have thin walls which are quite different from those of the caeca and which constitute a pre-caecal region of the gut. Where they join the caeca proper there is on each side a rosette-like tuft of six small diverticula. These can be seen in whole mounts of larger specimens but not in the smaller ones. They can however be seen in sections of specimen 9, which is slightly less than 0·5 mm. long. In specimen 15 the diverticula are about 40μ long and $22-27\mu$ broad, and their epithelium of slightly columnar cells $8-10\mu$ thick has the dense appearance of embryonic tissue. The diverticula arise at what is taken to be the origins of anterior extensions of the caeca, which are minute in these specimens.

The caeca are formed into enormous dilatations with intervening constrictions. Even in whole mounts, the internal epithelium evidently varies in thickness and is shallow in dilated, but tall in constricted regions, and of graded intermediate depth in intervening regions. In sections of specimen 15 more detail can be seen. In the constricted regions and nearby parts 20-25 tall cells measuring about $30\mu \times 2-3\mu$ can be counted in a 50μ extent of caecal wall. These cells tend to obliterate the lumen of the caecum. Their nuclei measure about $2\mu \times 1\mu$ and are not quite basal in position, the basal part of each cell comprising a clear zone containing a granule. The major part of each cell, internal to the nucleus, is finely granulated and entirely free from its neighbours. It terminates in a knob-like swelling. Towards the middle of each caecal dilatation the epithelium gradually becomes shallow, and here short cells measuring $3-5\mu \times 2-3\mu$ also become sparser, a 50μ extent of caecal wall on the average containing no more than about 8 of them.

This unusual caecal structure raises a number of interesting questions which cannot be answered by the study of a few preserved specimens. Are the caecal dilatations temporary or permanent? If temporary, as might be expected, what changes take place in the epithelium to restore the topographical differences observed when the gut has been emptied and refilled and when a new arrangement of dilatations and constrictions comes into being? Are tall cells reduced to short cells during digestion, and are short cells able in

some way to transform themselves into tall cells? The explanations can only come from a study of the functional morphology of the caeca, for which living specimens will be necessary. The caeca are provided with both circular and longitudinal muscle fibrils, though these are too fine to be measured in microns; where sections become tangential such fibrils are clearly seen to cross one another at right angles.

Other organs. The specimens are so immature that little can be stated concerning the reproductive system, and for study of the excretory system living specimens are necessary. The genital pore is a transverse, slit-like opening situated in the median plane in a deep fold just in front of the ventral sucker. At its rim, the cuticle and the subcuticular tissues are thickened, forming a small papilla. What are interpreted as the earliest rudiments of the gonads occur as transversely elongate strands of embryonic tissue a short distance behind the ventral sucker. What seem to be the earliest rudiments of the vitelline follicles occur in the region between the two suckers. No trace of vitelline follicles was found in the posterior region. The brain abuts on the posterior wall of the oral sucker, and on each side of the body there is a large nerve. The excretory canals form a Y-shaped arrangement in front of the excretory vesicle, and the posterior and antero-lateral canals show several loops in the transverse plane. All three canals are lined with cubical epithelium, and in parts of them traces of cilia can be seen.

Posterior appendages. The two posterior appendages provide the most distinctive character of this larval trematode. Each has its own slender connection with the body, the delicate stalk passing through the excretory pore to a point of attachment on the wall of the excretory vesicle. The two appendages are situated on right and left and they are generally almost equal in length, but specimen 13 has the longest appendage seen on one side (1.24 mm., or 1.47 mm. body-length), while its fellow is a rudiment (or vestige?) only 0.15 mm. long (Fig. 1D). This seems to have been a natural loss, whereas specimen 11 has lost one appendage and specimen 7 both appendages unnaturally. The largest specimen (15) seems to have reached a stage at which the appendages disappear, because specimen 14, which is slightly smaller, has very small, shrunken appendages.

A canal which extends down the entire length of each appendage is continuous with the caecum on the same side of the body.

The writer must confess to an initial scepticism regarding the appendages, which in length are disproportionate to the length of the body (Tables 1 and 2). His first reaction was to suspect that they represent varying degrees of prolapse of the caeca, perhaps as a result of abrupt fixation. Militating against this view is the fact that individuals with long appendages do not have correspondingly shorter caeca; indeed, the body seems to be as full of caecal dilatations as could well be (Fig. 1D). A study of sections shows that the appendages are not artifacts. Posteriorly, the caeca become markedly narrower and immediately internal to the opening of the appendage into the excretory vesicle the lumina of the caeca and the nuclei of the reduced walls can be seen neatly arranged one on either side of the posterior excretory canal, which enters the excretory vesicle in the median plane. In sections it is seen that the cuticle of the appendages is not smooth, but distinctly granular at the surface, and there is direct continuity with the cuticle of the excretory vesicle. The central lumen is here and there obliterated, vacuoles appearing in its place, yet it persists in some measure nearly to the posterior end of the appendage. The marginal one-third of each appendage consists of strongly eosinophilic masses of cytoplasm of a granular nature. However, this layer appears to be a continuation of the muscle layers of the body and what appear to be granules are probably muscle fibrils more or less obliquely arranged. There is no evidence of circular or longitudinal fibrils, but numerous nuclei are present in the cytoplasmic masses and these resemble the nuclei associated with the muscle layers of the body. A slight amount of parenchyma completes the histological structure of the appendage. Excretory vessels do not enter the appendages.

The variable length of the appendages in different individuals is a point difficult to explain, because it is unlikely to arise as a result of differences of muscular state. The enigma must persist however until living specimens appear, but the opinion can be expressed that in some way at present unknown the appendages assist flotation and serve to bring the larva from the vicinity of some bottom-dwelling mollusc in which earlier stages of development occur into the planktonic zone. Hutton (1954, Fig. 3) published a photograph of one specimen which seems to be a reproduction of an

earlier record (1952, Fig. 6) of a specimen which was found free in a plankton sample and which was named *Cercaria C.*

DISCUSSION

A few points concerning the specimens described by Hutton (1954) might be discussed briefly. These numbered 8 and they were obtained from 5,767 arrow-worms of three species—*S. enflata*, *S. hexaptera* and *S. lyra*. The incidence of infection was stated for these species as 0·9%, 0·14% and 1·15% respectively, but the numbers of hosts examined is not stated. From his Table 1 showing 8 different depths from the surface down to 350 metres it is clear that 8 arrow-worms had one parasite each.

Hutton's account is very brief and it contains measurements (in microns!) of only the smallest and the largest of the 8 specimens, which are as follows :—

	Specimens		
	small	large	
length of body	320 720
breadth of body	152 464
width of oral sucker	96 160
width of ventral sucker	112 208
length of R. appendage	160 384
length of L. appendage	160 256
width of R. & L. appendages	...	80	80

The range is thus less extensive than that for the writer's specimens, corresponding to the part covered by specimens 2–11 inclusive. Breadth is thus about one half of body-length in the small specimen, rather more than one half in the large specimen. The breadth of the oral sucker in small and large specimens is 30% and 22% body-length, the breadth of the ventral sucker 35% and 29% body-length. Both suckers seem to be relatively larger than in the writer's specimens but the same trend is seen for each, diminution in relative size with increase in size of the body as a whole. The appendages of Hutton's small and large specimens are 50 and 53% body-length on the right side, and 50 and 36% body-length on the left side, and no statement is made concerning any possible variation in length in other specimens.

Hutton observed and referred to the circular furrowing of the cuticle and also to a sub-cuticular layer "except at the extreme anterior end of the body". "Near the oral sucker, the layer separates from the cuticle and runs medially to the oral sucker". He refers his reader to Fig. 1, where this is shown, but the whole statement is erroneous. What he figures as subcuticular tissue leaving the integument and passing to the oral sucker is muscular tissue extending from the muscular layers to this sucker, an extrinsic muscle of the oral sucker. Hutton also described and figured erroneously a short oesophagus "bifurcating almost immediately into the intestinal caeca", and did not mention caecal diverticula, although he used both transverse and longitudinal sections. We do not know the sizes of specimens which were sectioned, however, and perhaps they were too small to reveal these structures.

SYSTEMATIC POSITION

It is unusual to attempt to refer a cercaria to its systematic position but in this instance two important characters enable us to make the attempt. The extension of the caeca into the appendages is taken by the writer as an indication that the corresponding adult will prove to be a trematode with anal openings situated in the wall of the excretory vesicle. This character occurs in members of various families but it seems to be a character of the seven genera of the Accacoeliidae. In one genus of this family each of the anterior extensions of the caeca has six diverticula, an unusual character which may be significant in the present instance. Judging by the occurrence of two unusual characters together it seems possible that *Cercaria owreae* is the larva of a species of *Accacladocoelium* Odhner, 1928. To which of four species it belongs cannot be decided, but the grotesquely pedunculate ventral sucker would seem to rule out *A. petasiporum* Odhner, 1928. The remaining three species are *A. nigroflavum* (Rudolphi, 1819), *A. macrocotyle* (Diesing, 1858) *sensu* Monticelli, 1893, and *A. alveolatum* Robinson, 1934. Dollfus (1935) separated the three species according to differences in the vitellaria, which are not developed as such in the writer's specimens. He also figured *A. nigroflavum* (Fig. 5-6) as a form with a finely furrowed cuticle and suckers situated rather near together. The same is true however of *A. alveolatum*, in which the cuticle around the excretory pore is modified to form anastomosing vertical ridges—a sort of "honeycomb" from which the trematode gets its specific

name. If these facts do not facilitate specific diagnosis at any rate they help to substantiate the generic diagnoses, which enables the writer to affirm that this corresponding adult is almost certainly a parasite of the sunfish *Mola mola* (L.).

SUMMARY

Cercaria owreae (Hutton, 1954) is renamed and redescribed. It has two posterior appendages and represents a new type of distome cercaria, named "Diplocercous". The caeca extend into the appendages, one into each, and a rosette-like group of six diverticula occurs at the anterior end of each of them. Certain peculiarities of the caecal epithelium are described and discussed briefly, but because of the immature state little information can be given about other organs. Fifteen larvae were obtained from 12 out of 181 *Sagitta hexaptera* collected in four Caribbean localities. Two larvae were found in the gut, the remainder in the coelom. The trematode probably belongs to the Accacoeliidae and is referred tentatively to the genus *Accacladocoelium* Odhner, 1928, adults of which are parasites of the sunfish *Mola mola* (L.).

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Observations on *Microfilaria fijiensis* Yeh, Symes and Mataika, 1958 from Fruit Bats (*Pteropus* *hawaiiensis*) in Fiji

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During the course of studies on human filariasis in Fiji in the period 1954-56, two new microfilariae were found in fruit bats. The first was found in the blood of 38 bats out of 111 examined from various islands of the territory. It has recently been described and named *Microfilaria fijiensis* by Yeh, Symes and Mataika (1958).

The second microfilaria was found near the end of the period of study in smears of the fluid from the peritoneal cavity of one fruit bat in which an adult filaria had been discovered in the abdominal space in the region of the kidney. This microfilaria is considerably smaller than the first. The adult filaria and the microfilaria found in the abdominal cavity are of the same species ; they have recently been described and named *Chiropterofilaria brevicaudata* by Yeh, Symes and Mataika (1958).

The observations here recorded concern only *Microfilaria fijiensis*, the adult of which has not yet been found.

Fluctuations in numbers of microfilariae (Mf. fijiensis) in the peripheral blood of fruit bats

Table I shows blood counts from four fruit bats made periodically over about 24 hours.

Blood was collected from a puncture made in the "costal" wing-vein, and prepared for examination by the usual technique—smeared on slides, dried, dehaemaglobinized, fixed, and stained with Geimsa.

There appear to be sharp fluctuations in numbers of microfilariae in the blood (as in the Pacific form of *W. bancrofti*). In two specimens highest counts were recorded at 10 a.m. and 10 p.m., in a third the peaks were at 3 a.m. and 1 p.m.

TABLE I

Fluctuations in numbers of microfilariae in 20 cmm. blood collected periodically over 24 hours from 4 Fruit Bats

Time of blood collection	No. 1	No. 2	No. 3	No. 4
1.00 a.m.				
2.00 a.m.	412	57		
3.00 a.m.			501	
4.00 a.m.				1
5.00 a.m.				
6.00 a.m.	98	66		
7.00 a.m.			346	1
8.00 a.m.				
9.00 a.m.			408	1
10.00 a.m.	637	153		
11.00 a.m.				
12 noon				
1 p.m.			499	1
2 p.m.	199	59		
3 p.m.			368	2
4 p.m.				
5 p.m.				
6 p.m.				
7 p.m.	284	143	213	2
8 p.m.				
9 p.m.			223	2
10 p.m.	520	213		
11 p.m.			338	Neg.
12 M.N.				

Possible Vector of Mf. fijiensis

It was thought that the vector of this filaria might be an ectoparasite of the fruit bat. There was apparently however, only one ectoparasite on the many bats examined—a large Nycteribiid kindly identified by Professor Theodor as *Cyclopodia inolita* Falcoz. Most bats had a few of these but usually not more than four or five.

Since these fruit bats live in the open, on large trees, without nests of any sort, there are no nest commensals (e.g. mites) to be considered as possible vectors.

Dissections were attempted of specimens of *Cyclopodia inolita* taken from infected bats. They are, however, so very tough that dissection became little better than a tearing apart and a teasing out of the tissues to facilitate microscopical search for developing forms of the filaria. None were seen, though they may have been present.

It was necessary to the main study concerning human filariasis (caused by *W. bancrofti*), to find out what animal filariae mosquitoes may carry, and to obtain from artificially infected mosquitoes enough material for comparison, to ensure that developing forms of animal filariae found in mosquitoes caught in houses or bush, should not be mistaken for those of *Wuchereria bancrofti*.

Mosquitoes of various species were therefore fed upon fruit bats infected with *Mf. fijiensis*. For most of the feedings the mosquitoes were merely released into a gauze cage (15 in. \times 15 in. \times 15 in.) in which an infected bat was confined. Since the bat's movements inside the cage were not restricted it was able to avoid heavy mosquito attack by frequent and rapid flapping of its wings. This destroyed many mosquitoes, and the recovery of fed mosquitoes was consequently very low. In a few of the later feedings the bat employed was anaesthetized before exposure. Recovery of fed mosquitoes was of course much higher by this method.

Attraction of captive mosquitoes to bat blood.

The numbers of species introduced to the experimental animals and the approximate percentages that were recovered after feeding are as follows :—

	<i>Used</i>	<i>Recovered</i>	
		<i>Fed</i>	<i>%</i>
<i>A. pseudoscutellaris</i>	...	1579	75%
<i>A. fijiensis</i>	...	740	34%
<i>A. polynesiensis</i>	...	258	80%
<i>A. aegypti</i>	...	249	61%
<i>A. vexans</i>	...	175	20%
<i>C. fatigans</i>	...	170	12%
<i>C. annulirostris</i>	...	280	25%
<i>C. sitiens</i>	...	150	33%

Of those that were not recovered many, both fed and unfed, in the early experiments escaped or were killed by the bats. Unfortunately records of the unfed specimens recovered were lost. If it

could be assumed that losses (through escape or death) were approximately similar for each species of mosquito used, then perhaps the figures above may be accepted as a very rough indication of the taste of the various species for bat blood.

On this assumption there appeared to have been some reluctance in all species except *A. pseudoscutellaris*, *A. polynesiensis* and *A. aegypti* to feed at all. These three are day-biting mosquitoes, and the first two are active in the bush and only rarely in houses. The other species are found in large numbers in houses where they bite mostly at night, though *A. vexans* and *A. fijiensis* are also known to bite humans readily out-of-doors at early dusk.

The habits of the day-biting bush mosquitoes and those of the day-resting fruit-bats would appear to coincide for the benefit of a mosquito-borne bat filaria.

Infection found in wild mosquitoes

During the study, considerable numbers of all species of mosquitoes found in houses and in bush were captured and dissected, and examined microscopically for the presence of developing forms of filariae (Symes 1955 ; 1957). In about 7,000 examinations, only one infection was discovered that could be reasonably referred to *Mf. fijiensis*. This occurred in a specimen of *A. polynesiensis* caught in the bush on Matuku Island. It is possible of course that some other of these infections were missed, or that they were included in the unidentified filariae recorded (Symes 1957) ; but if they were, their numbers are probably very small, mainly because mosquito collections were not made in the vicinities of bat colonies.

Laboratory infections in mosquitoes

Table II presents a summary of laboratory infections in mosquitoes. Infections in specimens that died during experiments are not included.

The numbers of specimens used, other than those of *A. pseudoscutellaris*, *A. fijiensis*, *A. aegypti* and *A. polynesiensis* are too small to produce significant results. Of these four, it is seen that all but *A. aegypti* tolerated development of the worm to maturity. But all rates of mature infection are low—about 14% in *A. pseudoscutellaris* and 8–9% in the others. (In similar experiments with *Wuchereria bancrofti* these species showed mature infection rates of 70–80%).

TABLE II
Summary of Laboratory Infections in Mosquitoes

Species of mosquitoes	No. of mosquitoes dissected	No. infected (all stages)	Micro-filaria	1st stage	2nd stage	3rd stage	Mature stage
<i>A. pseudoscutellaris</i>	769	371	76 (53.4)	120 (69.8)	75 (3)	67 (2.2)	33 (3)
<i>A. fijiensis</i>	94	8	4 (7.7)	2 (6)	0 —	1 (2)	1 (1)
<i>A. polynesiensis</i>	105	36	11 (14)	21 (1.9)	1 (1)	2 (5)	1 (1)
<i>A. aegypti</i>	120	12	7 (10)	5 (10)	0 —	0 —	0 —
<i>A. vexans</i>	26	2	2 (19)	0 —	0 —	0 —	— —
<i>C. faiigans</i>	14	0	— —	0 —	0 —	0 —	— —
<i>C. annulitarsis</i>	42	2	2 (7)	0 —	0 —	0 —	— —
<i>C. siiensis</i>	23	0	— —	0 —	0 —	0 —	— —

Where "0" is shown, dissections of specimens were made with negative results.

Figures in brackets are the average number of larvae per mosquito.

A. aegypti permitted a very slow development of the worm to first stage, many microfilariae being found up to the 13th day after the infective feeds. It would seem that this species is not tolerant to the development of the filaria.

Nothing may be deduced from the small samples of *A. vexans*, *C. fatigans*, *C. annulirostris* and *C. sitiens*.

Effect of different densities of blood infection upon the rates and densities of infections in mosquitoes

Results of infection of *A. pseudoscutellaris* fed upon bats with varying intensities of blood infections are shown in Tables III and IV. The figures are erratic, probably because of inadequate number of mosquitoes. They indicate as one would expect, a bigger pick-up of microfilariae from the heavier infections; and if mature stages are ignored, there may be a relationship between the higher production of second and third stage worms and the heavier blood infections, at least up to the 203 blood count.

Development of Mf. fijiensis in mosquitoes

Development in mosquitoes, where this proceeded, was similar to that of *W. bancrofti* in mosquitoes.

First stage : The ingested microfilariae having shortened and thickened during a period up to 24 hours (sometimes more) in the stomach, moved up to the thorax and there assumed well-developed "tails" whilst thickening and shortening still more to the approximate "sausage" shape of the first stages of *W. bancrofti*. "Tails" have been seen twenty-four hours after the infective feed.

These first stage forms were considerably smaller than those of *W. bancrofti*. Measurements of 28 specimens taken from several specimens of *A. pseudoscutellaris* two to five days after feeding were as follows :—

Length :	0·1 to 0·335 mm.	Average 0·178 mm.
Breadth :	0·014 to 0·037 mm.	Average 0·023 mm.
Tail :	0·015 to 0·034 mm.	Average 0·023 mm.

Development was apparently uneven and erratic. Full first stage growth was reached apparently in five days when larvae became about 0·3 mm. in length, and 0·03 mm. in breadth and in length of tail. Some specimens measured at two days development were 0·106 mm. long by 0·017 mm. broad; some of three days development were 0·136 mm. long by 0·022 mm. broad.

TABLE III
Laboratory Infections of *A. pseudoscutellaris* from bats with different blood counts.

Blood count per 20 cmm.	No. of Mosquitoes	% positive	% with microfilariae	% with 1st stage	% with 2nd stage	% with 3rd stage	% with mature stage
7-8	K 119	6.7	23	2.1 (1)	none exam'd.	0 [in 60]**	12 (1)
	D 36	2.8	20 (1)*	12 (1)	0 [in 10]	none exam'd.	none exam'd.
78	K 123	33	50	33	9.7	12.8	14 (3)
	D 53	28	100 (1)	50 (11)	28.5 (2)	5 (1)	none exam'd.
203	K 423	62	50	38	29	27.3	15 [28 in 183]
	D 51	51	61	15	22.6	29	11 [2 in 18]
533	K 104	57.7	60	52.8	50 (10)	14	12.3 [1 in 8]
	D 44	68	96	0 [in 8]	9 (1)	40 (4)	[0 in 5]

K = Mosquitoes killed immediately before dissection.

D = Mosquitoes that died during the 24 hours before dissection.

** Figures in square brackets are numbers of infections in mosquitoes examined at times considered approximately suitable for production of the stages concerned.

* Figures in curved brackets are actual numbers of mosquitoes infected.

TABLE IV
Intensities of Infections in Mosquitoes (*A. pseudoscutellaris*) fed upon different blood infections

Blood count in 20 cmm.	No. of Mosquitoes	Microfilariae	Average numbers of developing stages in mosquitoes infected			
			1st stage	2nd stage	3rd stage	Mature stage
7 : 8	K 119	1.5	1			4 (1)
	D 36	1	1			
78	K 123	3.5	2.7	2.6	1.5	1 (3)
	D 53	1	2.3	1	1 (1)	
203	K 423	3.3	7.5	2.6	2.5	2.7
	D 216	9	20.5	2.7	2	5
533	K 104	10	7.9	4.2	2 (3)	14 (1)
	D 44	17	—	4 (1)	2.5	

K = Mosquitoes killed immediately before dissection.

D = Mosquitoes that died during the 24 hours before dissection.

Figures in brackets are numbers of infected mosquitoes from which the average was obtained. They are shown only for particularly low numbers.

Specimens found in *A. pseudoscutellaris* after a delayed development of 10 days were from 0·094 to 0·108 mm. in length and 0·026 to 0·03 mm. in breadth. Living first stage larvae have been found in this mosquito on the twelfth day after the infective feed. Sometimes such backward specimens were found together with second and third stage worms.

Second stage: Second stage larvae, or what appear to be of this stage are not easy to describe. They are rather inactive, worm-like, with no obvious tail or papillae, considerably bigger than first stage and smaller than third stage, worms. They were usually found in the thorax. Of 16 specimens taken from twelve mosquitoes the lengths ranged from 0·185 to 0·5 mm. with an average of 0·362 mm., whilst breadths varied from 0·018 to 0·035 mm. with an average of 0·028 mm. They were recorded in *A. pseudoscutellaris* from the fifth to the fourteenth days after the infective feed.

Third stage: Third stages were much more active than the earlier stages (though not as lively as the equivalent stage of *W. bancrofti*). They occurred usually in the thorax, head and proboscis, though like *W. bancrofti* they were encountered also in the abdomen. They are distinguished by their relative size, their activity and by two pairs of papillae on the tail. One pair of these appears to be situated on a protuberance or a short lateral (or ventral or dorsal) tip of the tail. Of 15 specimens collected from thorax, head and proboscis of *A. pseudoscutellaris*, the length ranged from 0·431 to 0·824 mm. with an average of 0·638 mm. and breadth varied between 0·017 to 0·025 mm. with an average of 0·0216 mm. Mature specimens from the proboscis varied from 0·52 to 0·824 mm. in length and from 0·019 to 0·025 mm. in breadth. Third stage and mature specimens have been seen in *A. pseudoscutellaris* on the seventh to the fourteenth days after infective feeds.

Table V shows the periods at which developing stages were seen in *A. pseudoscutellaris*. It would seem from them and from the percentages of mosquitoes that fed on experimental bats (page 229) that none of the mosquito species used were good intermediate hosts for this filaria.

TABLE V

Days after infective feed on which developing stages were recorded. Numbers in brackets show the average number of worms per mosquito.

A. pseudoscutellaris

Days after feed	Micro- filarial	Number of mosquitoes with			
		1st stage	2nd stage	3rd stage	Mature
1	14 (5)	3 (4)			
2	3 (3)	3 (3)			
3	6 (1.7)	7 (4.3)			
4		3 (2.7)			
5	3 (1)	4 (3.7)	1 (7)		
6		2 (2)	2 (2.5)		
7		8 (3.1)	7 (4.3)	4 (1.5)	
8		5 (4)	5 (4.4)	3 (4.7)	
9			3 (2.7)	7 (1.7)	
10		6 (1.3)	7 (2)	4 (4)	
11			1 (5)	2 (3)	
12		3 (2)	6 (1.3)	8 (2)	4 (1)
13		3 (2)	4 (1.5)	7 (1.6)	
14		2 (2.5)	3 (1.5)	4 (1.7)	3 (1)

ACKNOWLEDGMENTS

Our thanks are due to all members of the Filariasis Research Unit for their interest and help in these observations.

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The Identification of Infective Filarial Larvae in Mosquitoes: with a Note on the Species Found in "Wild" Mosquitoes on the Kenya Coast

By G. S. NELSON

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During recent investigations on filariasis in Kenya it soon became apparent that little was known about the identification of filarial larvae in mosquitoes. The World Health Organisation Expert Committee on Filariasis (1957) recognised this gap in our knowledge and recommended that further research was needed in the differentiation of filarial larvae in their arthropod hosts.

Fifteen species of filarial worms from mammals are known to develop in mosquitoes; these include 4 species of *Wuchereria*, 6 *Dirofilaria*, 3 *Setaria* and 2 *Dipetalonema*. One bird filaria, *Aproctoides*, four species of *Foleyella* from frogs and a *Conispiculum* and *Oswaldo filaria* from lizards also undergo complete development in mosquitoes. There seems no doubt that many more will be found to be transmitted by mosquitoes in nature. It is therefore rather surprising to find only four references to filarial larvae of animals having been seen in mosquitoes during human filariasis surveys. Poynton and Hodgkin (1938) and Halcrow (1954) found a few larvae thought to be *Dirofilaria immitis*, Raghavan *et al.* (1952) found larvae of *Dirofilaria repens* and Carter (1948) found some very long infective larvae which he suggested may have originated from waterbuffaloes.

Faust (1949) records 73 species of mosquitoes as possible vectors of *Wuchereria bancrofti*; the incrimination of many of these is doubtful, being based on the assumption that the larvae found in "wild" mosquitoes are of human origin. Many workers have in fact assumed that it is not possible to distinguish the infective larvae of the human parasites from those of animals.

Although detailed laboratory studies have been carried out on the development of several species in mosquitoes, very few attempts have been made to apply this knowledge to epidemiological investigations. Recently Iyengar (1957) has reviewed some of this work and reproduced the illustrations of the infective larvae of *W. bancrofti* by Lebreiro (1905) and Kobayashi (1940) and those of *W. malayi* by Feng (1936); he also illustrates the infective larvae of *D. immitis*.

On the island of Pate, off the North East Kenya Coast, several larvae with quite distinctive morphology were found in mosquitoes in and around the village of Faza. In this localized area, seven species of filarial worms were present in the very limited domestic and wild animal population. The human population had a high infection rate with *W. bancrofti*. An attempt was made to identify the filarial larvae in the wild mosquitoes by comparing them with a collection of known infective larvae obtained by feeding mosquitoes on animals known to be infected with a particular species. In this way a "reference collection" of infective larvae was compiled and it was possible to identify with confidence several of the local species; we now have no difficulty in distinguishing the infective larvae of *W. bancrofti* from *W. patei*, *D. immitis*, *D. repens*, *D. corynodes* or *S. equina*.

In this paper no attempt has been made to describe the larvae in great detail, only those characters which were found useful in differentiation have been stressed. Thanks to the very generous help of Mr. Wharton in Malaya, it has been possible to include excellent specimens of the infective larvae of *W. malayi* and *W. pahangi* in the "reference collection", these species have therefore been described for the purpose of comparison.

A table has also been produced summarising existing information on the remaining species of filariae known to develop in mosquitoes.

MATERIAL AND METHODS

A general account of the investigation on the island of Pate with details of mosquito infection experiments has been published elsewhere (Heisch *et al.* 1959).

Infective larvae from freshly dissected mosquitoes were fixed in 70% alcohol containing 5% glycerine, and mounted in a very small drop of the fixative on a coverslip which was then inverted over a cavity slide and sealed with "Euparol". This method preserves the larvae with very little distortion; the external features are usually clear but the internal structures are not clearly defined.

It is not always convenient to dissect mosquitoes in the field ; a technique was therefore developed for the dissection of preserved mosquitoes. Freshly killed mosquitoes were preserved in 80% ethyl alcohol (hot alcohol being preferred for histological work) ; when convenient they were transferred through descending dilutions of alcohol to water, stained for three days in Mayer's acid haemalum, differentiated three days in distilled water and then transferred to glycerine to await dissection. The stained insects were dissected in the glycerine. The infective larvae are easily picked out and mounted in the same medium under a coverslip and ringed with "Euparol". This method which is a modification of that used by Lebied (1950) has several advantages over the methods usually employed. The external and internal characters of all stages of larvae are well defined, the dissection can be carried out in the laboratory under the best conditions, and the position and number of the larvae in the mosquito can be determined accurately. If the mosquitoes are dehydrated and cleared in terpineol, beautiful sections can be made and mounted in Canada Balsam. These sections clearly show all the stages of development of the larvae in the mosquito. We have used the staining technique as a routine method in our filariasis investigations along the Kenya Coast. The technique is equally useful in onchocerciasis investigations (Nelson, 1958), and with this method good preparations of the infective larvae of *Loa loa* have also been made from *Chrysops* experimentally infected by Dr. B. O. L. Duke in the Cameroons. Unfortunately the stained specimens mounted in glycerine gradually fade ; several other mounting media have been tried but all have caused some distortion of the larvae.

A binocular microscope is essential for dissecting and mounting. The morphological characters are often clearly seen with a $\frac{1}{6}$ in. objective but for measuring and detailed study of the caudal extremities a $\frac{1}{12}$ in. oil immersion objective with a micrometer eyepiece is necessary.

This paper is not concerned with the identification of first and second stage larvae but only with the third stage or infective larvae. It has been shown by Newton and Pratt (1945) and Wharton (1957) that third stage larvae from the abdomen move rapidly to the proboscis when the mosquito starts feeding. Third stage larvae are regarded as infective whether they occur in the proboscis or elsewhere in the mosquito host. These larvae have a well developed cuticle, they are usually very active, they have lost the skin of the second ecdysis and there is no sign of an anal plug.

TABLE I
MEASUREMENTS (IN μ) OF INFECTIVE FILARIAL LARVAE FROM EXPERIMENTALLY INFECTED MOSQUITOES

Filarial species	Mosquito host	Technique	Number measured	Mean length	Mean breadth	Mean distance anus to caudal extremity	Mean breadth halfway anus to caudal extremity	Mean breadth	Mean breadth	Mean anal ratio
<i>W. bancrofti</i>	<i>C. faijans</i>	glycerine	19	1329	20.8	58.0	14.5	4.0	4.0	4.0
	<i>M. uniformis</i>	haemalum	10	1409	24.4	63.2	15.6	4.1	4.1	
	<i>M. longipalpis</i>	glycerine	17	1592	24.8	57.5	14.9	3.9	3.9	
		haemalum	4	1410	22.7	46.7	12.7	3.6	3.6	
<i>W. pahangi</i>	<i>A. orthurans</i>	haemalum	10	1200	24.0	45.8	15.6	2.9	2.9	
		glycerine	20	1593	21.8	57.7	13.8	4.1	4.1	
		haemalum	14	1330	18.9	47.7	13.2	4.3	4.3	
<i>W. palei</i>	<i>Ae. pembaensis</i>	glycerine	16	1631	24.4	62.0	13.1	4.7	4.7	
	<i>M. uniformis</i>	glycerine	10	1444	22.9	60.5	13.6	4.5	4.5	
	<i>M. africanus</i>	glycerine	10	1448	24.7	56.1	12.1	4.6	4.6	
<i>D. coronodes</i>	<i>Ae. pembaensis</i>	haemalum	10	1468	22.0	56.2	12.6	4.5	4.5	
	<i>Ae. aegypti</i>	glycerine	16	881	22.4	33.6	18.2	1.8	1.8	
		glycerine	20	935	22.4	37.9	18.7	2.0	2.0	
		haemalum	20	820	19.3	38.6	16.5	2.3	2.3	
<i>D. immitis</i>	<i>M. africanus</i>	glycerine	10	878	20.9	39.2	17.6	2.2	2.2	
	<i>C. faijans</i>	glycerine	20	976	21.9	35.4	17.6	2.0	2.0	
	<i>Ae. pembaensis</i>	glycerine	13	1530	26.5	46.0	16.7	2.7	2.7	
<i>S. equina</i>	<i>Ae. aegypti</i>	glycerine	40	1584	26.9	44.6	17.2	2.6	2.6	

CHARACTERS USED IN IDENTIFICATION

It will be seen in Table I that *length* is an important character for differentiating the infective larvae, e.g. *Dirofilaria* spp. which average less than $1,000\mu$, can be immediately distinguished from *Wuchereria* spp. and *Setaria* which average more than $1,400\mu$.

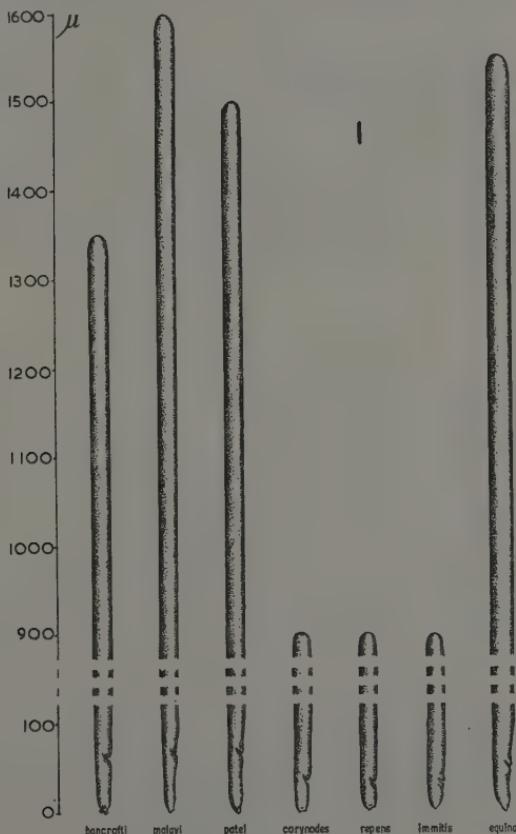


Fig. 1. Relative lengths of infective larvae of seven species occurring in mosquitoes.

This difference is clearly shown in Fig. 1. Various factors affect the length of the larvae; if they are dissected out several days after they have reached maturity they are usually longer than larvae removed on the day following the second ecdysis; on the other hand,

in mosquitoes with a very heavy infection physical crowding results in some of the larvae being shorter than normal. Another important factor affecting the length is the species of mosquito host ; Kartman (1953) has shown that the larvae of *D. immitis* are longer in *C. quinquefasciatus* than in *Ae. aegypti*. In our experiments the larvae of *W. patei* were longer in *Ae. pembaensis* than in *Mansonioides*.

It is not possible to measure the active living larvae, usually they are measured after being fixed and mounted. With the alcohol-glycerine method there is little shrinkage but with the staining technique especially if the larvae have been fixed with hot alcohol, there is often considerable shrinkage, this probably accounts for the shorter larvae of *W. malayi* and *W. pahangi* after haemalum staining as seen in Table I. These various factors are probably responsible for the considerable differences recorded for the length of various filarial larvae in the literature.

The position of the anus is an important feature in differentiation ; the anal aperture is much nearer the caudal extremity in *Dirofilaria* than in *Wuchereria* and the position of the anus in *Setaria* is intermediate. This feature together with the differences in shape of the larvae between the anus and the extremity have been used by Wharton (1957) to differentiate *W. malayi* from *D. immitis* ; he calculated what he has called the "Anal ratio" which is the distance from the anus to the caudal extremity divided by the breadth of the larva half way between those two points. This ratio is useful if only fragments of larvae are available for examination or if the terminal anatomy is not very clear. The "Anal ratio" in *Dirofilaria* averages approximately 2, in *Wuchereria* the ratio is nearer 4.

The most useful character for differentiating the larvae is *the shape of the caudal extremity*. With very little experience it is possible to recognise even with the low power objective, the cigar shaped end of *Dirofilaria*, which clearly distinguishes it from *Wuchereria* which has a much more definite narrowing between anus and extremity. Most species of infective larvae have three caudal papillae with one, usually the most prominent, dorsal ; the other two are in a lateral or ventral position. The number, shape and size of these papillae are of importance in differentiation. The papillae are often very small and can only be seen by differential focussing under high magnification.

IDENTIFICATION OF SPECIES

W. BANCROFTI (Cobbold, 1877)

Host : Man. Development in mosquitoes was first demonstrated by Manson (1878).

Infective larvae have been examined from *C. fatigans*, *A. gambiae*, and *A. funestus* and measured as follows :—

Length : 1,170 μ —1,575 μ ; breadth : 18 μ —32 μ ; anus to caudal extremity, 56 μ —72 μ .

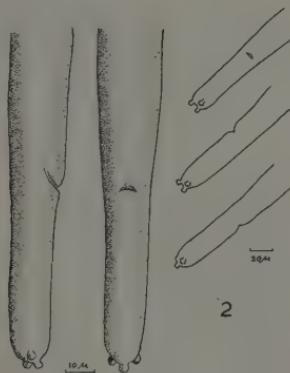


Fig. 2. Caudal end of infective larvae of *Wuchereria bancrofti*.

The three bubble-like caudal papillae on the rounded extremity of the infective larvae of *W. bancrofti* are quite characteristic, they are large, equal in size, nearly spherical and at times, they appear to be pedunculated rather like miniature electric light bulbs. (Fig. 2). All three papillae are not always obvious, their relative prominence depends upon the position in which the larva is mounted. There is a slight narrowing of the larva of *W. bancrofti* between the anus and rounded extremity which gives the posterior end of the larva the appearance of a knobbed club.

The infective larva was well illustrated by Manson (1878). Iyengar, R. (1956) has emphasized the size of the papillae in an illustration showing three large cow-like teat knobs on the caudal extremity, he gives the length of the larvae as between 1,300 μ and 1,700 μ . Iyengar, M. O. T. (1957) has reproduced the illustration of Lebreiro (1905) which shows a caudal morphology with much smaller

papillae, an appearance which might easily be confused with *D. corynodes*. Kobayashi (1940) gives the average length as $1,617\mu$; he found some infective larvae as short as 936μ .

W. MALAYI (Brug, 1927)

Hosts : Man, cat, monkey (*Macaca irus*), rhesus monkey (*M. rhesus*), slow loris (*Nycticebus coucang*), civet cat (*Viverra tangalunga*). Development in mosquitoes was first demonstrated by Brug (1931).

Infective larvae have been examined from *M. uniformis* and *M. longipalpis* fed on man and measured as follows :—

Length : $1,280\mu$ — $1,720\mu$; breadth : 22μ — 28μ ; anus to caudal extremity : 42μ — 64μ .

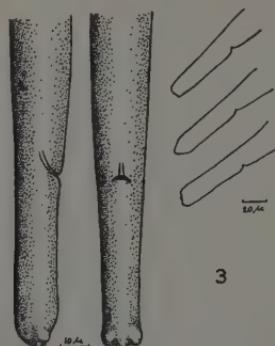


Fig. 3. Caudal ends of infective larvae of *Wuchereria malayi* or *W. pahangi*.

The infective larva of *W. malayi* has three poorly defined caudal papillae more in the nature of slight bulges of the cuticle than true papillae. The whole caudal extremity is more tapered and less rounded than *W. bancrofti*; if the caudal extremities are examined with an oil immersion lens, these species are easily separated.

Feng (1936) gives the average length as $1,304\mu$; his illustrations of the infective larvae emphasise the narrowing of the caudal extremity. Poynton and Hodgkin (1938) note the poorly developed caudal papillae but say the larvae are very similar to *W. bancrofti*. Iyengar, R. (1956) gives the length as $1,300\mu$ — $1,650\mu$; in his

description of the stages of development of *W. bancrofti* and *W. malayi* he omits to illustrate the infective larvae of *W. malayi*. Wharton (1957) found that the larvae of *W. malayi* varied from $1,235\mu$ — $2,000\mu$ in length; he says that "a practised observer can usually distinguish between *W. bancrofti* and *W. malayi* by the greater prominence of the terminal papillae in *W. bancrofti*."

W. PAHANGI Buckley and Edeson, 1956

Hosts : Dog, cat, tiger (*Panthera tigris*), civet cat (*Viverra tangalunga*), slow loris (*Nycticebus coucang*), wild cat (*Felis planiceps*). Development in mosquitoes was first demonstrated by Edeson and Wharton (1957).

Infective larvae have been examined from *Armigeres obturbans* fed on a cat and measured as follows :

Length : $1,280\mu$ — $1,720\mu$; breadth : 17μ — 24μ ; anus to caudal extremity 42μ — 63μ .

No consistent differences have been seen between this larva and *W. malayi*.

W. PATEI Buckley, Nelson & Heisch, 1958

Hosts : Cat, dog, genet (*Genetta tigrina*), bush-baby (*Galago crassicaudatus*). Development in mosquitoes was first demonstrated by Heisch *et al.*, 1959.

Infective larvae have been examined from *Ae. pembaensis*, *M. uniformis* and *M. africanus* fed on a cat, and measured as follows :

Length : $1,200\mu$ — $1,800\mu$; breadth : 20μ — 28μ ; anus to caudal extremity 44μ — 68μ .

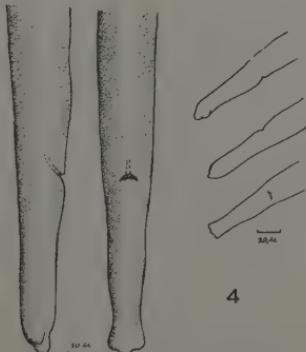


Fig. 4. Caudal end of infective larvae of *Wuchereria patei*.

The caudal extremity of the infective larva is very similar to that of *W. malayi* but usually the dorsal protuberance is more pronounced giving the larva a Depezzier catheter appearance in the dorso-ventral position, and resembling a dog's head in the lateral position. The larva narrows more definitely between the anus and extremity; the anal ratio is therefore usually greater than in *W. malayi*.

This species which was found in cats and dogs on the island of Pate by Nelson and Heisch (1957), is closely related to *W. malayi* and *W. pahangi*; the microfilariae are of the *malayi*-type and the adults are very similar (Buckley *et al.*, 1958). Although large numbers of infective larvae of this species have been found in *Ae. pembaensis* coming to bite man, no microfilariae have been found in the human population. *W. patei* has recently been found in domestic cats and bush-babies near the Tana river on the Kenya mainland.

DIROFILARIA CORYNODES (Linstow, 1899), syn. *D. aethiops* Webber,
1955

Hosts: Monkeys (*Cercopithecus aethiops* and *Colobus* sp.). Development in mosquitoes was first demonstrated by Webber (1955).

Infective larvae have been examined from *Ae. pembaensis* and *Ae. aegypti* fed on a monkey and measured as follows:—

Length: 680μ – $1,000\mu$; breadth: 20μ – 28μ ; anus to caudal extremity 28μ – 40μ .

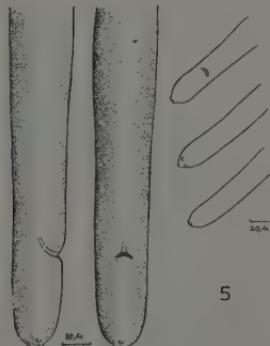


Fig. 5. Caudal end of infective larvae of *Dirofilaria corynodes*.

The infective larvae of *D. corynodes* have the typical cigar-shaped tail of *Dirofilaria* with much less pronounced narrowing between the anus and the extremity and with the anus much nearer the extremity than in *Wuchereria*. There are three small papillae clustered together at the end of the larvae giving the caudal tip a rather flattened appearance. Often only two papillae are visible.

Webber (1955) has studied the development of this species in *Ae. aegypti*; she gave the length of the infective larvae as varying from 600μ to $1,000\mu$ the majority being between 700μ and 800μ . Having noted the obvious difference in length between this species and *W. malayi*, Webber remarks that "The larval forms of filarial worms are more easily differentiated by the characteristics of their life cycles than by their morphology". This is not true for the differentiation of the infective larvae in mosquitoes which can be found in any part of the mosquito's anatomy. It is admitted that the earlier stages of development of *Wuchereria* are to be found only in thoracic muscles but so also are those of *Setaria*, and although *D. immitis* and *D. repens* only develop in the malpighian tubules it is unusual to find the infective larvae still *in situ*. Even if only the terminal part of the infective larvae of *D. corynodes* was available for examination there should be no difficulty in distinguishing it from the *Wuchereria*, *Setaria* or other species of *Dirofilaria*. The distance from the anus to caudal extremity together with the anal ratio and the three small papillae are quite diagnostic.

DIROFILARIA REPENS (Railliet and Henry, 1911).

Hosts : Dog, cat, genet cat (*Genetta tigrina*), lion (*Leo leo*).

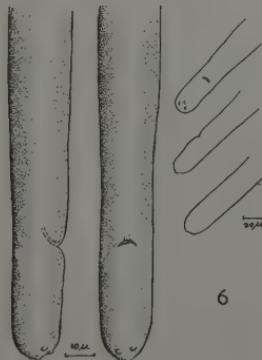


Fig. 6. Caudal end of infective larvae of *Dirofilaria repens*.

Development in mosquitoes was first demonstrated by Fulleborn (1908).

Infective larvae have been examined from *Ae. pembaensis*, *Ae. aegypti*, *M. uniformis* and *M. africanus* fed on a cat and measured as follows :—

Length : 640μ — $1,080\mu$; breadth : 16μ — 25μ ; anus to caudal extremity 34μ — 44μ .

The infective larva of *D. repens* is very similar to that of *D. corynodes* but instead of three terminal papillae there is only one; this terminal papilla is very small. Two even smaller papillae are situated subterminally on the ventral surface a short distance from the extremity, usually only one of these is visible. If the larva is lying in the dorso-ventral position the extremity may appear to be completely smooth.

Gunewardene (1956) gives a good illustration of *D. repens* infective larvae; in one of her photographs the subterminal papilla is clearly defined; she found the infective larvae varied in length from 900μ — $1,015\mu$.

DIROFILARIA IMMITIS (Leidy, 1856)

Hosts : Dog, dingo (*Canis dingo*), maned wolf (*Chrysocyon brachyurus*), fox (*Vulpes vulpes*). Development in mosquitoes was first demonstrated by Grassi and Noé (1900).

Infective larvae have been examined from *Ae. pembaensis*, *Ae. aegypti* and *C. fatigans* fed on a dog and measured as follows :—

Length : 800μ — $1,040\mu$; breadth : 18μ — 26μ ; anus to caudal extremity : 26μ — 40μ .

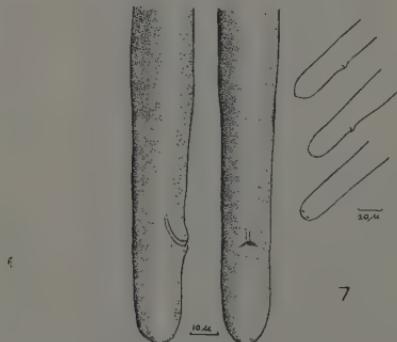


Fig. 7. Caudal end of infective larvae of *Dirofilaria immitis*.

The infective larvae of *D. immitis* cannot usually be distinguished from *D. repens*. In the limited number of specimens examined two slight differences have been noted : the subterminal papillae are smaller in *D. immitis* and the anal aperture is often situated on a slight prominence.

Dogs are often simultaneously infected with several filarial species ; one of our animals was found at autopsy to have large numbers of adult worms of *W. patei*, *D. immitis*, *D. repens* and a *Dipetalonema* sp. During life only the microfilariae of *D. immitis* and *W. patei* were found in the peripheral blood. The larvae measured in Table I were from *C. fatigans* fed on a dog in which only *D. immitis* adults were found at autopsy. (*C. fatigans* is not a vector of *D. repens*.) There is always a danger of misinterpretation of mosquito feeding experiments due to incorrect identification of microfilariae.

It was most surprising to find the infective larvae of *D. immitis* and *D. repens* so much alike, especially as there is no difficulty in distinguishing either the adult worms or the microfilariae of these two species. It is worth noting that in general the size of infective larvae is in no way related to either the size of the microfilariae or the parent worm.

Manson's advice in his "Tropical Diseases" that "Anyone desirous of working out for himself the metamorphosis of the filaria in mosquitoes can readily do so even in the absence of a suitable human subject by setting anopheline mosquitoes to bite filariated dogs" has borne fruit in recent years. *Dirofilaria immitis* is probably the best known filaria in the laboratories through the world. Notable studies on transmission have been carried out by Noé (1901), Roubaud (1937), Summers (1943), Kartman (1953), Kershaw *et al.*, (1953), Stueben (1954) and Webber & Hawking (1955) but the morphology of the infective larvae has received little attention.

Poynton and Hodgkin (1938) have illustrated the essential differences between the infective larvae of *D. immitis* and *W. bancrofti* and *W. malayi*. Kartman (1953) has shown that the average length of the infective larvae is 850 μ and breadth 25 μ . He found the maximum length was 1,200 μ in *C. fatigans* but only 950 μ in *Aedes aegypti*. Iyengar (1957) has illustrated the infective larvae of *D. immitis* and he notes that there is a single rounded terminal papilla and "very rarely an additional but smaller papilla may be seen just behind the terminal papilla". Yeh (personal communication) has confirmed that there are in fact two very small sub-terminal papillae in this species.

SETARIA EQUINA (Abildgaard, 1789)

Host : Horse, mule and donkey. Development in mosquitoes was first demonstrated by Heisch *et al.*, 1959.

Infective larvae were examined from *Ae. aegypti*, *Ae. pembaensis* and *C. fatigans* fed on donkey and measured as follows :—

Length : 1,280 μ –1,720 μ ; breadth : 21 μ –28 μ ; anus to caudal extremity 40 μ –52 μ .

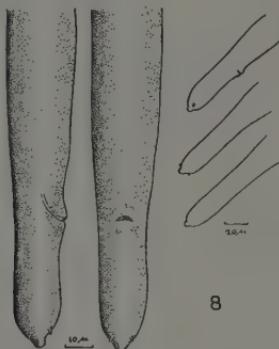


Fig. 8. Caudal end of infective larvae of *Setaria equina*.

The infective larva of *S. equina* is easily distinguished from the other species ; it has one large terminal papilla with two small subterminal papillae which look like miniature ears. The whole larvae has a robust appearance.

Setaria spp. are widely distributed throughout the world and many species of the adults have been described. The author has been unable to trace any detailed description of the development of a *Setaria* in its arthropod host. Lapage (1956), Chandler (1955) and Levashov (1946) have suggested that Tabanids are vectors of some of the *Setaria*. Innes and Shoho (1953) however, record that Japanese workers have successfully infected *Anopheles hyrcanus*, *Armigeres obturbans* and *Aedes togoi* with *S. digitata* of cattle and Kadenatsii (1956) has infected *Culex pipiens* with *S. marshalli* of sheep. Shoho (1958) had no difficulty in infecting mosquitoes with *S. digitata* in Ceylon.

On the island of Pate in Kenya we frequently encountered infective larva in *Aedes pembaensis* and *Ae. aegypti* which possessed characteristic sub-terminal "horns" or "ears" in the tail region ;

The following key may assist field workers to differentiate infective larvae found in wild-caught mosquitoes. It is hoped that the collection, preservation and detailed study of infective larvae from other areas will help towards a better understanding of the epidemiology of many other filarial infections.

KEY TO THE DIFFERENTIATION OF INFECTIVE FILARIAL LARVAE
IN MOSQUITOES

1. Caudal papillae or protuberances present..... 2
- No caudal papillae..... 9
2. Length more than $1,100\mu$ 3
- Length less than $1,100\mu$ 6
3. Three equal bubble-like caudal papillae..... *W. BANCROFTI*
- Three caudal papillae of various shapes and size..... 4
4. Terminal or dorsal papilla prominent
- All three papillae poorly developed; anal ratio less than 4.5 *W. malayi* and *W. pahangi*
5. Terminal dorsal papilla "dog's nose" shape; lateral papillae poorly developed; larva narrows between anus and extremity; anal ratio averages 4.5..... *W. PATEI*
- Terminal papilla large and central; two small lateral sub-terminal alae; anal ratio less than 3 *S. EQUINA*
6. Anus more than 50μ from extremity..... 8
- Anus less than 50μ from extremity..... 7
7. Three small terminal papillae *D. CORYNODES*
- One small terminal papilla with or without two very small subterminal papillae *D. IMMITIS* or *D. REPENS*
8. Three prominent terminal papillae *D. ARBUTA*
9. Length usually less than $1,100\mu$; anus less than 50μ from extremity..... *FOLEYELLA* spp.
- Length $1,000\mu$ - $1,250\mu$; anus more than 50μ from extremity *C. FLAVESCENS*

it was suspected that it might be *Setaria* as the vectors of all other species of filaria in the village of Faza other than the dog *Dipetalonema*, had been accounted for. Eventually an infected donkey was purchased and feeding experiments confirmed that *Aedes pembaensis* and *Ae. aegypti* were good hosts of *S. equina* and excellent specimens of the infective larvae were added to the "reference collection". An infective larva similar to, but larger than that of *S. equina* was seen in a few *Ae. pembaensis*. It is suspected that this may be the bovine *Setaria*. It is also possible that the very long infective larvae seen by Carter (1948) in Ceylon are from the *Setaria* of water buffaloes. Mosquitoes may prove to be the main intermediate hosts of all species of *Setaria*.

*
RECORDS OF 14 OTHER SPECIES OF FILARIAL WORMS KNOWN TO DEVELOP IN MOSQUITOES
(Infective larvae not available for study)

Filarial species	Definitive host	Development in mosquito first described by	Mosquito host	Remarks
<i>Setaria digitata</i>	<i>Bos taurus</i>	Japanese workers (unpublished)	<i>A. hyrcanus</i> <i> Ae. togoo</i> <i> Arm. obturbans</i>	Reported by Innes & Shoho (1953)
<i>S. marshalli</i>	Sheep	Kadintatsii (1956)	<i>Culex pipiens</i> <i> Aedes sp.</i>	—
<i>Dirofilaria scapiceps</i>	<i>Lepus americanus</i>	Highby (1943, a)	<i>Aedes spp.</i>	Not illustrated
<i>D. spinosa</i>	<i>Erythizon dorsatum</i>	Highby (1939)	<i>Aedes stimulans</i>	—
<i>D. tenuis</i>	Raccoon	Pistey (1956)	<i>Aedes</i> <i> taeniorhynchus</i> <i>?Anopheles quadrimaculatus</i>	—
<i>Dipetalonema diacantha</i>	<i>Erythizon dorsatum</i>	Highby, (1939)	<i>Aedes spp.</i> <i>Mansonia perturbans</i>	—
<i>D. arbuta</i>	<i>Erythizon dorsatum</i>	Highby, (1943, b)	<i>Aedes spp.</i>	Illustrated by Highby (1943, b)
<i>Aproctoides lissum</i>	<i>Francolinus pondicerianus</i>	David, (1955)	<i>C. fatigans</i>	Later reported by Raghavan and David (1955)
<i>Conispiculum flavescens</i>	<i>Calotes versicolor</i>	Pandit et al (1929)	<i>C. fatigans</i>	Illustrated by Pandit et al (1929)
<i>Oswaldo filaria chlamydosauri</i>	<i>Chlamydosaurus kingii</i>	Bancroft & Mackerras (unpublished)	<i>C. fatigans</i> <i>C. annulirostris</i>	Reported by Johnston & Mawson (1923) and Mackerras (1953) : not illustrated
<i>Foleyella dolichoptera</i>	<i>Rana sphencephala</i> <i>Rana pipiens</i>	Causey (1939, a)	<i>Ae. aegypti</i> <i>C. fatigans</i> <i>C. pipiens</i>	Not illustrated
<i>F. ranae</i>	<i>R. calamitanus</i> <i>R. catesbeiana</i>	Causey (1939, b)	<i>Ae. aegypti</i> <i>C. fatigans</i> <i>C. pipiens</i>	Measurements and illustrations from Kotcher (1941)
<i>F. brachyoptera</i>	<i>R. pipiens</i> <i>R. sphenocephala</i>	Causey (1939, c)	<i>Ae. aegypti</i> <i>C. fatigans</i> <i>C. pipiens</i>	Measurements and illustrations from Kotcher (1941)
<i>F. duboisi</i>	<i>R. esculenta</i>	Wittenberg & Gerichter (1944)	<i>C. molestus</i>	Illustrated by Wittenberg and Gerichter (1944)

* I have recently heard from Mr. C. B. Symes that whilst working in Fiji between 1954 and 1956 he successfully infected *Aedes pseudoscutellaris*, *Aedes polynesiensis* and *Aedes fijiensis* with a filarial parasite (? sp.) from the fruit bat *Pteropus hawaiiensis*. The infective larvae measured 520μ-850μ with an average length of 700μ. They are said to have four terminal papillae "two of which appear to be more prominent than the others." (See also Symes & Mataika, *J. Helminth.*, 1959, 33, 223-232.)

INFECTIVE FILARIAL LARVAE IN "WILD" MOSQUITOES FROM THE KENYA COAST

In the course of the present epidemiological studies on filariasis along the Kenya coast large numbers of mosquitoes are being dissected. The results of the investigation at Faza on the island of Pate have already been published (Heisch *et al.* 1959). The author has had an opportunity of examining all the infective larvae found in more than 18,000 dissections ; 243 mosquitoes contained infective larvae ; and analysis of the species identification is given in Table III.

Infective larvae of *W. bancrofti* have been seen in *C. fatigans*, *A. gambiae* and *A. funestus*. These mosquitoes were all collected from inside houses. The two unidentified specimens in *C. fatigans* were distorted in mounting ; one specimen was possibly *S. equina*. *C. fatigans* is known to be a good host of several filarial species ; although it is predominantly anthropophilic it is probable that elsewhere it will be found infected with non-human filariae.

Infective larvae of *W. patei* were found in *Ae. pembaensis*, *M. uniformis* and *M. africanus*. At one time it was thought that *Ae. pembaensis* might be an important vector of *W. bancrofti* in Kenya (Heisch *et al.*, 1956). This mosquito is a voracious manbiting species and it has been found with a consistently high filarial infection rate, both in houses and in the bush. It is now known that *Ae. pembaensis* does not carry infective larvae of *W. bancrofti* and experiments have shown that *W. bancrofti* will not develop in this mosquito. This is rather surprising in view of the known versatility of *Ae. pembaensis* as a filarial host. In the laboratory we have had no difficulty in infecting *Ae. pembaensis* with *W. patei*, *D. corynodes*, *D. repens*, *D. immitis* and *S. equina* ; in nature it has been found infected with all these species together with several quite distinct species as yet not identified. On the island of Pate, dogs, cats and genet cats are often infected with both *W. patei* and *D. repens* ; several *Ae. pembaensis* have been found with mixed infections and there has been no difficulty in distinguishing the larvae.

In a village on the mainland where the *Mansonia* were found infected with *W. patei* there was a *W. bancrofti* infection rate in the local population of 15% but no *C. fatigans*, *A. gambiae* or *A. funestus* were found in the houses. Without a knowledge of the morphological characters of the infective larvae we might easily have made the mistake of incriminating *Mansonia* as a vector of *W. bancrofti*.

TABLE III
SPECIES OF INFECTIVE LARVAE IN "WILD" MOSQUITOES FROM THE KENYA COAST

Mosquito	Number dissected	Number with infective Larvae	<i>W. bancrofti</i>	<i>W. patei</i>	<i>D. coronoides</i>	<i>D. immitis</i>	<i>S. equina</i>	Not Identified
<i>C. fatigans</i>	2,800	49	47	0	0	0	0	2
<i>A. gambiae</i>	1,020	6	6	0	0	0	0	0
<i>A. funestus</i>	925	9	9	0	0	0	0	0
<i>Ae. pectinifer</i>	8,750	166	0	54	16	47	29	20
<i>Ae. aegypti</i>	2,850	10	0	0	0	7	1	2
<i>M. uniformis</i> or <i>M. africanus</i>	2,100	3	0	3	0	0	0	0

Subsequent investigations revealed that cats and bush babies in this village were infected with *W. patei* and both *M. africanus* and *M. uniformis* proved to be excellent vectors.

The infective larvae of *S. equina* were found in *Ae. pembaensis* and *Ae. aegypti*; the earlier stages develop in the thoracic muscles and are indistinguishable from *W. bancrofti* and superficially the infective larvae might be mistaken for those of *W. bancrofti*. Bertram *et al.* (1958) have warned against the possibilities of confusing *W. bancrofti* with *Setaria* species in mosquitoes in the Gambia.

Ae. aegypti has been infected with *W. bancrofti* in the laboratory (Henrard *et al.*, 1946) and is listed by Faust (1949) as an important vector in nature. Nearly 3,000 *Ae. aegypti* from houses in the endemic filariasis areas of Kenya have been dissected, none have been found carrying the infective larvae of *W. bancrofti*, although several contained larvae of *D. immitis* or *D. repens*. Here again, without a knowledge of the characteristics of the infective larvae, it would have been easy to conclude erroneously, that *Ae. aegypti* was a vector of *W. bancrofti* in that region.

DISCUSSION

Filarial worms are widespread and very common parasites successfully adapted to a great variety of hosts ranging from frogs to elephants. New species are being found every year: the vectors of the vast majority are unknown. The above account has shown that in the few species known to use mosquitoes as their intermediate host, the infective larvae can be fairly easily distinguished. On the Kenya coast we can say with some confidence that particular mosquitoes are infected in nature with particular filarial parasites.

Now that we are sure of the morphological characters of the infective larvae of *W. bancrofti* it will be possible to determine accurately the infection rates and intensity of infection of this parasite in its insect vectors. Unless there is complete confidence in the identification of filarial larvae in their vectors it is useless to apply mathematical formulae to help interpret the data collected in filariasis surveys. The "potential transmission index" used by Kessel (1957) is meaningless unless one can exclude with certainty non-human filarial infections in the mosquitoes examined. Many mosquitoes thought to be transmitting parasites of man are probably only concerned in the transmission of filarial parasites of animals.

The same is probably true for the other filarial parasites of man. In a sample of *Simulium neavei* from an endemic onchocerciasis area in Uganda the author has found two quite distinct species of infective larvæ; one of these is much smaller than the infective larva of *O. volvulus* and may be a filarial parasite of birds. Anderson (1956) has recently shown that Simuliidae in Canada are vectors of the *Ornithofilaria* of domestic and wild ducks. Gordon (1958) has also suggested that many of the larvae in *S. damnosum* in the onchocerciasis areas of West Africa are not parasites of human origin.

The work of Buckley (1938) in Malaya on the *Culicoides* vectors of *O. gibsoni* also supports the idea that filarial larvae in insect vectors are rarely pure infections; he found three distinct species of infective larvae in the suspected vectors of this bovine *Onchocerca*.

Unless the human filarial parasites are studied as part of a biological complex involving several related species often sharing the same intermediate hosts many mistakes will be made not only in the identification of the true vectors but also in the assessment of the relative importance of the various insect species involved in transmission.

SUMMARY AND CONCLUSIONS

1. At least twenty-two species of filarial worms are known to develop in mosquitoes. Filarial larvae of non-human origin must often be present in mosquitoes dissected during filariasis surveys yet the larvae seen are commonly assumed to be of human origin.

2. On Pate island off the Kenya coast where bancroftian filariasis is prevalent, several distinct species of infective larvae were found in mosquitoes both in the houses and in the bush. Seven species of filarial worms were found in the local animals and a collection of known infective larvae was made by feeding mosquitoes on these different infections. A study of the material in this "reference collection" showed that many of the larvae in "wild" mosquitoes could be identified with confidence.

3. A technique has been developed for the dissection of preserved and stained mosquitoes; this method has many advantages and can be used in routine filariasis surveys.

4. The characters which were most useful in differentiating the infective larvae were: the length; the position of the anus; and the shape of the caudal extremity. Eight species of infective larvae were available for study, these are described and illustrated:

W. bancrofti, *W. malayi*, *W. pahangi*, *W. patei*, *D. corynodes*, *D. repens*, *D. immitis* and *S. equina*. The literature dealing with a further fourteen species is reviewed.

5. A simple key has been produced to help identify the species of infective larvae found in mosquitoes.

6. On the Kenya coast *W. bancrofti* infective larvae have been found only in *C. fatigans*, *A. gambiae* and *A. funestus*. Infective larvae of animal origin which might easily be mistaken for those of *W. bancrofti* have been found in *Ae. pembaensis*, *Ae. aegypti*, *M. uniformis* and *M. africanus*.

7. Formulae for transmission indices based on infection rates in insect vectors are of little value unless there is confidence in specific identification.

8. A study of the infective larvae in *Simulium neavei* from an onchocerciasis area in Uganda has shown that not all the larvae are of human origin. A closer examination of the morphology of infective larvae in the vectors of filarial parasites of man in other areas will almost certainly show that the interpretation of infection rates may be complicated by the presence of infections of non-human origin.

9. Feeding experiments were carried out with *Aedes pembaensis* and *Ae. aegypti* on a donkey infected with *Setaria equina*; both of these mosquitoes proved to be suitable vectors of this filarial worm.

ACKNOWLEDGMENTS

I am particularly indebted to Dr. R. B. Heisch for his critical advice and stimulating encouragement, and to Professor Buckley for his personal assistance and constant interest throughout this investigation. The majority of mosquito dissections have been carried out by Mr. Mikael Ikata, his help has been invaluable. I would like especially to acknowledge the generous help of Mr. R. H. Wharton of Kuatan Malaya and Mr. G. R. Barnley of Uganda. I am grateful to Mr. C. W. A. Guggisberg for his assistance with the illustrations.

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On a New Species of the Genus *Thelazia* Bosc 1819, from a Hooded Vulture (*Necrosyrtes* *monachus*) from Uganda

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The writer received from Mr. F. R. N. Pester (Department of Parasitology) a small collection of helminths that had been collected in Uganda from a hooded vulture in November 1958. These proved to be a new species of the genus *Thelazia* Bosc, 1819. They are described and named herein as *T. ugandensis* n.sp.

Eight males and nine females were present. The buccal cavity is wider than long and devoid of any teeth. The mouth is simple with a hexagonal opening. Of the cephalic papillae, six small papillae surround the mouth and four pairs are submedian in position; there is one pair of laterally situated prominent amphids. The cuticle is transversely striated; the striations are not well marked in the posterior part of the body. The oesophagus is not very clearly divided into glandular and muscular parts.

THELAZIA UGANDENSIS n.sp.

Male

The body length varies between 16-20 mm. and the width 0.54-0.57 mm. The buccal cavity measures 0.03-0.033 mm. in depth and 0.04 mm. in width. The oesophagus is 0.8 mm. long. From the anterior extremity the cervical papillae are situated at a distance of 0.6-0.7 mm. and the nerve ring at 0.4-0.5 mm.

The spicules are very unequal in length. The right spicule, measuring 0.26-0.27 mm. is small and stout, with a rounded tip. The left spicule is long and filiform with a conical and alate tip. It measures from 3.6-3.9 mm. in length. A small gubernaculum is present and measures 0.09 mm. in length.

There are 22 precloacal papillae, 11 on the left side, 10 on the right side and 1 median unpaired papilla anterior to the cloaca. The postcloacal papillae are 5 pairs as figured (Fig. 4). The tail is bluntly rounded.

Female

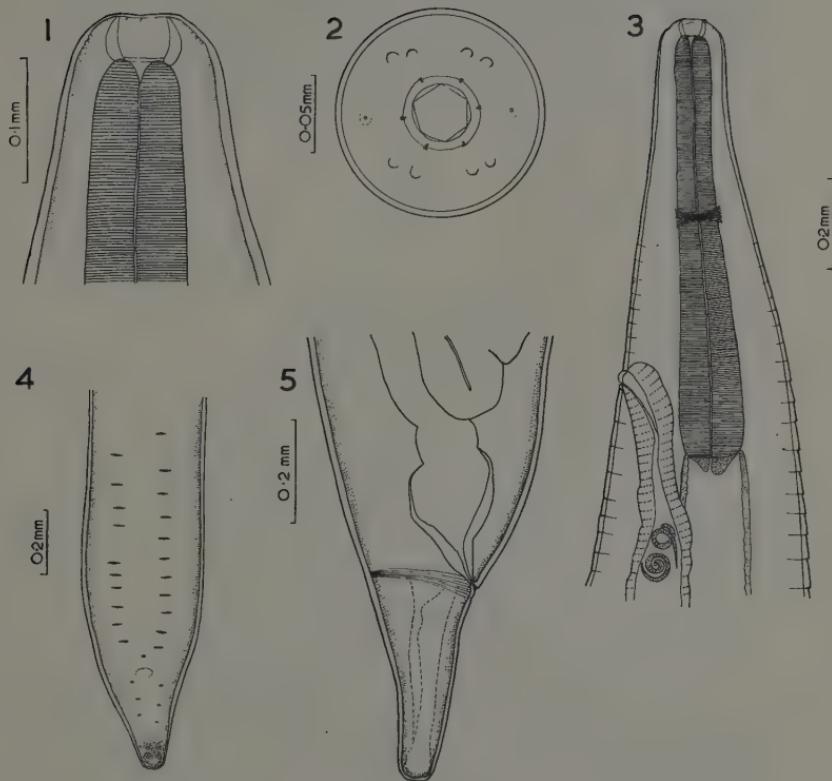
The length of the body is 20–24 mm. and the width 0·65–0·67 mm. The buccal cavity is 0·033–0·04 mm. deep and 0·04–0·05 mm. wide. The length of the oesophagus is 0·78–0·86 mm. The cervical papillae are situated at 0·5–0·6 mm. from the anterior end. The nerve ring lies at a distance of 0·4 mm. from the anterior end.

The vulva is very prominent and is located at 0·65–0·84 mm. from the anterior end. It is found at the level of the end of the oesophagus or slightly anterior to it. The vagina, full of embryos, is followed by a long tube which gives rise to two uteri running parallel to each other. The anus is situated at a distance of 0·36–0·39 mm. from the posterior extremity.

DISCUSSION

More than twenty species of *Thelazia* have been described from avian hosts. Some of the species are described only from female specimens as *T. cholodkowskii* Skrjabin, 1922 and *T. anolabiata* (Molin, 1860) Railliet et Henry, 1910, and some species are very inadequately described. It is not possible to compare the new species with the incompletely described species in all the details; however *T. ugandensis* differs from the other known species of the genus mainly in having a very long left spicule and also in the number and arrangement of the caudal papillae of the male. The maximum length of the left spicule recorded is in *T. platyptera* Hwang and Wehr, 1957 and in *T. campanulata* (Molin 1858) Railliet et Henry, 1910. But in both the above species it is not more than 2·7 mm. long. In *T. dentifera* Sandground, 1933, the length of the left spicule is given as 0·29 mm., but it seems to be a misprint because in the figures given it appears to be much longer and is, probably, 2·9 mm. *T. ugandensis* differs from *T. dentifera* in the body length of both the sexes and the arrangement of the caudal papillae of the male.

T. depressa Baylis, 1920, was originally described from *Mungos fasciatus*. It was later recorded by Baylis (1934) from *Sarcogyps calvus*, thus establishing the occurrence of *T. depressa* in vultures. Vuylesteke (1953) recorded *T. depressa* from *Necrosyrtes monachus pileatus*. *T. depressa* Baylis, 1920, as described by Schuurmans-Stekhoven (1937) from *Buteo rufofuscus augar* differs from its



Thelazia ugandensis sp.nov.

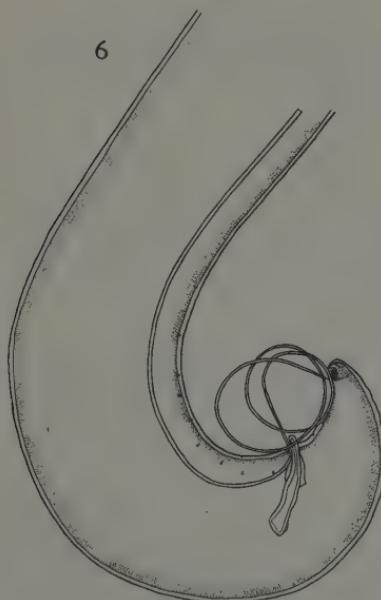
Fig. 1.—Anterior extremity, lateral view. Fig. 2.—End-on view of head. Fig. 3.—Anterior region of female, lateral view. Fig. 4.—Ventral view of male tail. Fig. 5.—Lateral view of female tail.

TABLE 1

	<i>T. dentifera</i> Sandground, 1933	<i>T. platyptera</i> Hwang & Wehr, 1957	<i>T. campanulata</i> (Molin 1868) Railliet et Henry, 1910	<i>T. agnignicanda</i> Schuurmans- Stekhoven, 1937	<i>T. depressa</i> Baylis, 1920	<i>T. ugandensis</i> n.sp.
Length (Body)						
Male	11	14	17	14	8.5	16-20
Female	13.5	17	16-25	21	11.5	20-24
Width	0.35 and 0.37	0.41 and 0.43	0.4 and 0.5-0.6	1	0.5	0.57 and 0.67
Length of Spicules						
Right	0.18-0.21	0.183-0.203	0.19	0.5	0.26-0.27	
Left	2.9 (?)	2.68-2.69	2.67	2.7	3.6-3.9	
Caudal Papillae of male						
Pre-anal	8-7 pairs 1 median	7 on left 8 on right 1 median	7 pairs 1 median	10 pairs 1 median	9 or 9 pairs 1 median	10 on right 11 on left
Post-anal	4 pairs	6 pairs	1 single and 3 pairs	4 pairs	5 pairs	1 median 5 pairs
Gubernaculum	Absent	0.06	Absent	Present		0.09
Anterior end—vulva distance	0.48	0.675	0.35			0.65-0.84
Host	<i>Picus canus hessei</i>	<i>Buteo platyptera</i>	<i>Falco magnirostris</i>	<i>Sarcogyps calvus</i>	<i>Halcyon chelicuti</i>	<i>Necrosyrtes monachus</i>
Geographical distribution	China	U.S.A.	Brazil	Africa (Belgian Congo)	Belgian Congo	Uganda

All measurements in millimeters.

original description (Baylis, 1920). Schuurmans-Stekhoven mentioned the presence of spines on the cuticle in the specimens obtained from *Buteo rufofuscus augar*. There are no spines on the cuticle in Baylis's description of *T. depressa*. The only known species of *Thelazia* possessing spines is *T. papillosa* (Molin, 1860) Railliet et Henry, 1910. On further examination, it may perhaps be found that Schuurmans-Stekhoven's specimens belong to *T. papillosa*.



Thelazia ugandensis sp.nov.

Fig. 6.—Lateral view of male tail.

(Same scale as for Fig. 3.)

T. digiticauda Schuurmans-Stekhoven, 1937 is described from the Belgian Congo, from *Halcyon chelicuti*. *T. ugandensis* differs from *T. digiticauda* in the larger body length and the presence of gubernaculum (length of the spicules is not given for *T. digiticauda*).

In the accompanying table *T. ugandensis* is compared with the above-mentioned species.

On the difference of these characters it is regarded as a new species and is named *T. ugandensis* n.sp.*

Host : *Necrosyrtes monachus* (Hooded Vulture).

Location : Eye.

Locality : Uganda.

ACKNOWLEDGMENTS

The writer is much indebted to Mr. F. R. N. Pester, of the Department of Helminthology, London School of Hygiene and Tropical Medicine for the material and to Professor J. J. C. Buckley, under whose guidance the work was carried out. Thanks are also due to Dr. P. L. LeRoux and Dr. L. S. Yeh for their kind help and advice.

SUMMARY

Thelazia ugandensis n.sp. is described from a hooded vulture. It differs from the other known species in the length of the spicules, length of the gubernaculum and the number and position of male caudal papillae.

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* After the present paper was received for publication a revision of the species of *Thelazia* from birds was published by Anderson, R. C. and Diaz-Ungria, C., (1959). They described a new species *T. tejerai*, redescribed some inadequately known species and gave a key to the 14 species. *T. ugandensis* differs from them all, mainly in the length of the left spicule.

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On a New Trematode, *Astiotrema sudanensis*, sp. nov., from a Freshwater Turtle in the Sudan

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and Tropical Medicine*

Seven specimens of this new species were collected from the intestine of a freshwater turtle, *Trionyx triunguis* (= *T. nilotica*) in the Sudan.

These are lanceolate worms which gradually taper to rounded ends, with a length of 2.5-2.9 mm. and a width of 0.6-0.9 mm. The cuticle is invested with scales, dense in the anterior half of the worm, but becoming more and more sparse towards the caudal end. The oral sucker is large, measuring 0.23-0.27 mm. in diameter and is about one and a half times the diameter of the ventral sucker which measures 0.14-0.17 mm. in diameter. Both suckers lie in the anterior half of the body. The mouth is subterminal and leads to a pharynx which is stout, 0.7-0.8 mm. by 0.11-0.12 mm., and leads to a long oesophagus of 0.25-0.32 mm. in length. The caeca terminate at the posterior border of the posterior testis or slightly anterior to it.

The testes are smooth, more or less rounded, and diagonal in position; the anterior testis is to the right and measures 0.22-0.30 mm., by 0.28-0.38 mm., and the posterior testis to the left measuring 0.28-0.35 mm. by 0.30-0.40 mm. The cirrus sac is large, 0.51-0.60 mm. in length, and extends posteriorly as far as the level of the ovary. It encloses a large seminal vesicle, a long pars prostatica surrounded by prostate cells, and a short cirrus. The genital atrium is immediately preacetabular, a very short distance posterior to the intestinal bifurcation.

The roughly spherical ovary is situated to the left side and measures 0.16-0.21 mm. in diameter. The seminal receptacle is pear-shaped. The follicular vitellaria extend along the lateral fields, but sometimes overlap the intestinal caeca, occupying an area between the middle of the oral sucker to the level of the posterior border of the anterior testis. The uterus descends between the testes to the caudal end of the worm before ascending to the genital pore. Eggs are numerous, elongated, thin shelled, measuring 29-31 μ by 8-10 μ .

DISCUSSION

Prior to the review of the genus *Astiotrema* by Yeh and Fotedar (1958), the genus, according to published works, contained 21 species. These two authors proposed to transfer *Astiotrema emydis* Ejsmont, 1930, to *Leptophallus*. Of the remaining species, their studies have shown that only four species were valid. These are :—

1. *Astiotrema reniferum* (Looss 1898) Looss, 1900.
2. *Astiotrema impletum* (Looss, 1899) Looss, 1900.
3. *Astiotrema monticelli* Stossich, 1904.
4. *Astiotrema odhneri* Bhalerao, 1936.

The only difference of importance reported by Yeh and Fotedar (1958) between *A. reniferum* and *A. odhneri* is the extension of the intestinal caeca. The writer studied specimens collected from the intestine of the freshwater turtle *Trionyx triunguis* in the Sudan and found that in some of the specimens the caeca terminate near the posterior extremity of the worm, in other specimens they terminate at the posterior border of the posterior testis. There were ranges in between these two extremes as well. This leads to the conclusion that *A. odhneri* is a synonym of *A. reniferum*. In fact Odhner (1911) when he first found that species described it as *A. reniferum*. The other differences described by Bhalerao (1936) regarding the shape and lobulation of the testis were shown later by Yeh and Fotedar (1958) to be of no value. Dr. Yeh (personal communication) agrees with this synonym.

A. reniferum was reported from only one fish, *Clarias batrachus* from Burma and India. The writer found it also in the intestine of the freshwater fish, *Clarias lazera* in the Sudan. This is the first time it has been reported from that host.

In 1958 also another species was reported by W. A. Siddiqui, namely *Astiotrema geomysia* from the intestine of the tortoise *Geoemyda spinosa*. This species does not fit in with the key of the genus given by Yeh and Fotedar, and gives us four valid species so far.

As it was not possible to assign the species under consideration to any of the four species mentioned above, it is considered to be a new species for which the name *Astiotrema sudanensis* is proposed.

A. sudanensis sp. nov. resembles *A. reniferum* to some extent, but differs from it in the relative size of the two suckers, the extension of the vitellaria and the smaller size of the eggs.

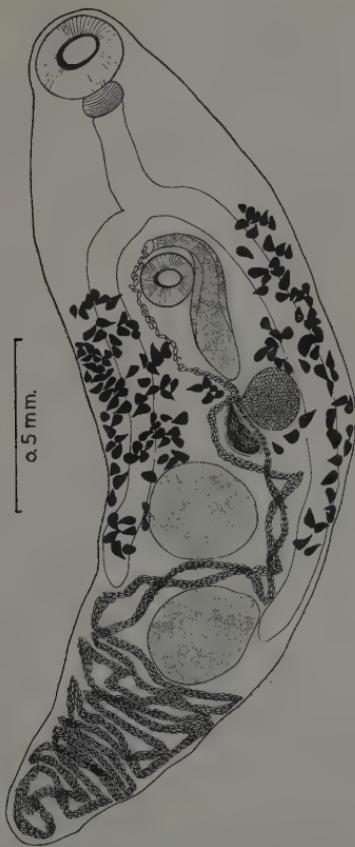


Fig. 1. *Astiotrema sudanensis* sp. nov. Ventral view.

ACKNOWLEDGMENTS

I wish to express my gratitude to Professor J. J. C. Buckley under whose guidance the work was done ; to Professor H. Sandon of the University of Khartoum for his guidance regarding the methods of collection and technique and to Dr. L. S. Yeh for his interest in the study.

KEY TO THE SPECIES OF ASTIOTREMA

1. Oral and ventral suckers roughly of equal size..... 2
Oral suckers larger than ventral sucker..... 3
2. Caeca terminating about the middle of body, vitellaria restricted to second quarter of the body, intestinal bifurcation posterior to ventral sucker..... *A. monticelli*
Caeca longer than above, vitellaria more dispersed intestinal bifurcation anterior to ventral sucker..... *A. reniferum*
3. Genital pore not posterior to intestinal bifurcation *A. impletum*
Genital pore posterior to intestinal bifurcation..... 4
4. Vitellaria extending from the middle of the ventral sucker *A. sudanensis* sp.nov.
Vitellaria extending from the level of the cirrus sac *A. geomysidia*

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**On *Ptychobothrium cypseluri* n.sp. (Cestoda :
Pseudophyllidea) from the Flying Fish, *Cypselurus
poecilopterus* caught off Waltair**

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Adult tapeworms infesting the spiral valve of elasmobranchs in Indian waters have received much attention (Southwell, 1930; Subramaniam, 1939, 1940; Ramavarma Raja, 1948; Kambata and Bal 1952, 1953, 1954; Subhaprada, 1951, 1955b; Rao, 1957), but comparatively little is known about those found in marine teleosts (Shipley, 1901; Rao, 1954; Ganapati and Rao, 1955; Subhaprada, 1955a). The recovery of specimens of the genus *Ptychobothrium* from the intestine of the flying fish *Cypselurus poecilopterus* taken in coastal waters at Waltair, Andhra Pradesh, provided an opportunity to remedy this deficiency to some extent.

MATERIAL AND METHODS

Specimens (10-15) removed from the intestinal mucosa of the host by gentle scraping in sea water were relaxed in tap water and fixed in 5% formalin or Bouin's fluid. For histological examination, 8-12 μ sections were stained with Ehrlich's haematoxylin and eosin and the PAS techniques, whilst whole mounts were stained with alum carmine.

DESCRIPTION

The cestodes ranged from 6-60 mm. in length, the shorter specimens being immature and probably representing recent infections. The scolex is arrow-head shaped (Fig. 1), 1.4-1.6 mm.

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long, 0·3 mm. broad anteriorly and 0·8 mm. at its base, without an apical disc, and the bothridia have ruffled margins. The strobila bears transverse furrows between which there may be four to eight true proglottids according to the number of reproductive units. The first 30–40 mm. of the strobila has proglottids with only anlagen of the reproductive organs (Fig. 2), and then ripe segments follow (Fig. 3). Gravid proglottids are rectangular, 1·3–1·6 mm. long and 1·1–1·2 mm. broad. The median genital pore opens on the dorsal surface whilst the uterine pore opens on the ventral side in a similar position.

Globular testes vesicles 55–68 in number (Fig. 2, T) are arranged as two distinct groups on either side of the median line. The oval cirrus sac lies slightly to the left or right of the midline, some 0·33 mm. anterior to the ovary. The ovary (Fig. 4, OV), though compact, is deeply lobulated. The ovicapt (OC) arises from the middle anterior and continues as the oviduct to meet the conspicuous receptaculum seminis (RS) which receives the vagina (V), a slender curved tube from the genital pore. The fertilization canal (FC) conveys the fertilized ovum from the receptaculum seminis to the ootype. The vitelline follicles are numerous and distributed amongst the bundles of longitudinal muscles. The conspicuous transverse vitelline ducts (TV) open at the level of the ovary into a median vitelline reservoir (VR), which in turn opens into the ootype. The ootype (OT) is a short robust tube with a cellular wall, whose proximal region is surrounded by the Mehlis' gland cells (MG). The uterus when replete with eggs appears as a large V-shaped sac (Fig. 3, UT) occupying the entire medullary region of the proglottid, and pushes itself into the segment ahead as far as the ovary. The thin-shelled eggs are non-operculate. Those found at the beginning of the uterus measure $0\cdot04 \times 0\cdot03$ mm., but as they pass up into the uterine sac development occurs and the eggs become larger until their dimensions are $0\cdot05 \times 0\cdot04$ mm. Yamaguti (1934) observed a similar condition in the case of *P. belones*.

DISCUSSION

The genus *Ptychobothrium* Loennberg, 1889 is represented by the one species *P. belones* (Dujardin, 1845) recorded in teleosts from various regions. (Joyeux and Baer, 1936; Wardle and McLeod, 1952). *Dibothrium restiforme*, described by Linton in 1891 from *Tylosurus caribbaeus* at Woods Hole, Massachusetts, is generally

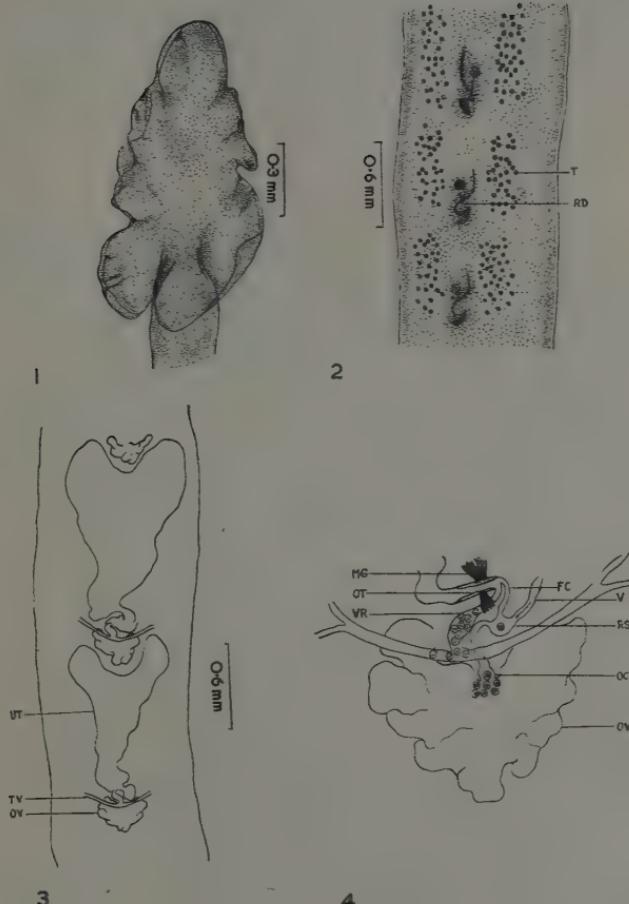


Fig. 1.—Scolex. Fig. 2.—Anterior proglottids showing testes vesicles (T) and rudiments of the reproductive system (RD). Fig. 3.—Ripe proglottids with V-shaped uterine sac (UT). OV=Ovary; TV=Transverse vitelline duct. Fig. 4.—Diagram showing the ovary and the reproductive ducts. FC=Fertilization canal; MG=Mehlis' gland; OC=Oocapt; OT=Ootype; OV=Ovary; RS=Receptaculum seminis; V=Vagina; VR=Vitelline reservoir.

believed to be *Ptychobothrium belones*, Linton (1934) described small immature specimens from *Exocoetus volitans* as *Bothriocephalus* sp., but in view of the similarities between his description and that given here it may well be that he was dealing with the present genus. Yamaguti (1934) identified *P. belones* from *Tylosurus schismatorhynchus* on the Pacific coast off Mie Prefecture, whilst Shuler (1938) recorded the species from *Tylosurus raphidoma* (Ranzani) from Tortugas, Florida.

The species described here differ from *P. belones* in the following manner. The ovary is deeply lobulate rather than non-lobulate. The uterus is not highly coiled, and the sinuous portion occupies relatively little space, while most of the medullary region is occupied by the conspicuous V-shaped sac. Yamaguti (1934) described an "S" curve in the initial stages in *P. belones* which becomes very sinuous when filled with eggs, occupying the entire medullary parenchyma, and develops at its distal end a sharply differentiated uterine sac. The testes vesicles, 55–68 in number, are far more numerous than in *P. belones*, where only 20 are present. Although similar in other respects, these differences are sufficient for regarding the present specimens as constituting a new species.

Host : *Cypselurus poecilopterus* Cuv. & Val.

Location : Intestine.

Locality : Waltair, Andhra Pradesh, India.

Type : Author's collection.

SUMMARY

1. A new species of the genus *Ptychobothrium* Loennberg 1889, recovered from the intestine of the flying fish *Cypselurus poecilopterus* Cuv. and Val., off the coast of Waltair, is described.
2. *Ptychobothrium cypseluri* n.sp. differs from *P. belones* (Dujardin, 1845), the only other known species of the genus, in the nature of the ovary, uterus and the number of testes.

ACKNOWLEDGMENTS

The author holds a Scholarship granted under the Colombo Plan by the Government of the United Kingdom. Thanks are due to Professor E. A. Spaul for facilities and helpful criticism.

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A New Tapeworm, *Inermicapsifer rhodesiensis* sp. nov. from a Scaly Ant-eater, *Manis temminckii*, in Southern Rhodesia

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Four worms were recovered from the intestine of a Scaly Ant-eater, *Manis temminckii*, examined in this Department in August, 1958. They appear to represent a new species for which I propose the name *Inermicapsifer rhodesiensis*.

ANOPLOCEPHALIDAE Cholodkovsky, 1902, emended Fuhrmann, 1907.

LINSTOWIINAE Fuhrmann, 1907

Inermicapsifer Janicki, 1910

Inermicapsifer rhodesiensis sp. nov.

The worms are medium sized, 80 mm. to 105 mm. in length, with a maximum diameter of 1.43 mm.

The scolex is 0.364-0.388 mm. in diameter and is provided with four suckers, diameter 0.13-0.18 mm., but entirely lacks a rostellum and therefore has no hooks. There is a short neck region, 0.28-0.31 mm. in diameter, and 1.1-1.8 mm. long. The segments are much wider than long, but the fully gravid segments tend to become square in outline.

The genital pores are unilateral and are situated in the middle or slightly anterior to the middle of the lateral border of the segment.

The excretory system consists of anastomosing dorsal and ventral canals. There are two pairs of prominent ventral canals, and one pair of dorsal canals.

The lateral nerves are broad and well defined, lying outside the lateral excretory canals.

The male and female organs appear simultaneously at about the 25th segment. An average immature segment is 0.11 mm. \times 0.44 mm. wide, and an average mature segment 0.42 mm. \times 1.15 mm. wide.

The testes vary in number both from one individual worm to another, and in different segments of the same worm. They are situated posteriorly in the segment, but they extend anteriorly in

the aporal region of each proglottid. The poral testes are all posterior to the genital ducts. The aporal and poral groups of testes are united in a continuous row behind the ovary. The number of poral testes varies between 9–12; the former figure is the number usually present. The number of aporal testes varies between 24–30, and has no consistent number. The total number of testes present is between 33–40. In a whole mount the testes appear circular and have a diameter of 0·035–0·038 mm.

The vas deferens is very convoluted, lies in the anterior poral region of the segment, and does not form an external seminal vesicle before entering the cirrus sac.

The cirrus sac is fairly small, being 0·113–0·129 mm. long and 0·047–0·050 mm. wide. It occupies about 1/10th of the total width of the segment. The cirrus is armed, 0·013 mm. in diameter, and 0·071 mm. long. The cirrus sac opens into a small genital atrium.

The vagina opens into the genital atrium posteriorly to the cirrus sac, and passes, together with the vas deferens, between the excretory vessels. Near the ovary the vagina widens into a spindle shaped receptaculum seminis.

The ovary is at first small, and in the poral 1/3rd of the segment. As it increases in size it sends out lateral lobes. The vitelline gland is small, compact, situated slightly aporally compared with the ovary, roughly spherical in shape, granular in appearance, and has a diameter of 0·07–0·072 mm.

The fertilised eggs are distributed throughout the segment. Each egg is surrounded by a membrane, and later each egg is enclosed within a parenchymatous capsule. The number of eggs per capsule is 5–9, and the number per segment 9–11.

Host : *Manis temminckii.*

Locality : Near Salisbury, Southern Rhodesia.

Type to be deposited in the British Museum (Nat. Hist.).

As Mahon, (1954) has pointed out, the genus *Inermicapsifer* represents a very unstable group of tapeworms whose specific characters are very variable and ill defined. The variation within one species of any one character may even overlap that of a related species. A specific determination therefore depends on a consideration of several characters. Mahon (1954) in an attempt to find a relatively constant character, estimated the various proportions between the dimensions of segments and other organs.

Representatives of this genus have, with two exceptions, so far been confined to two groups of mammals, the Rodentia and the Hyracoidea. The species found in each group are specific to that order of mammals. The two exceptions mentioned above have both been found in man. *Inermicapsifer cubensis* Kouri, 1938, bears a close resemblance to *I. arvicanthidis* (Kofend, 1917), which was recovered from a native child in Kenya and was described by Baylis (1949). This latter form had previously been known from African rodents. Baer, Kouri, and Sotolongo (1949) believed that the two

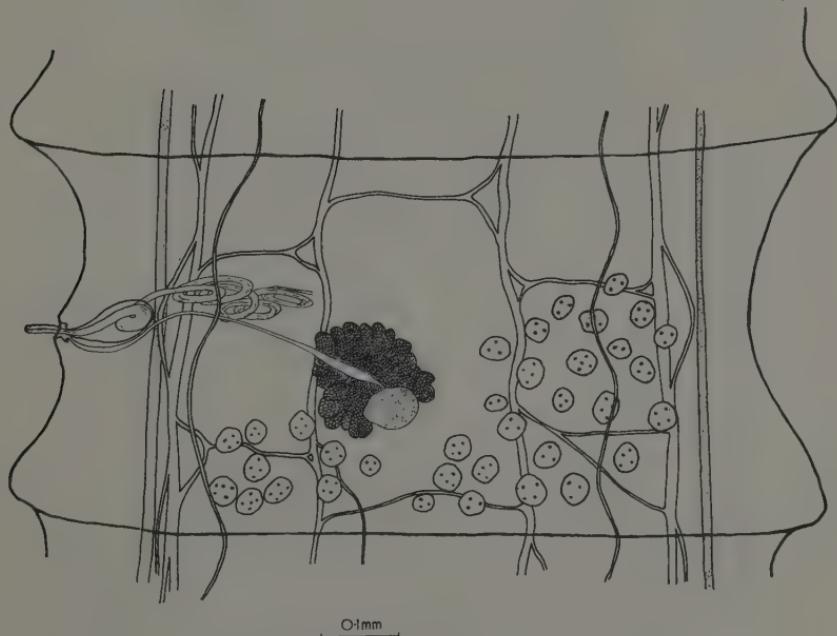


FIG. 1.—Mature segment of *Inermicapsifer rhodesiensis* sp. nov.

species could be separated on the basis of the number of egg capsules per segment and the size of the cirrus-sac. However Baylis (1949) and Fain (1950) thought that the two forms were identical. Joyeux and Baer (1949) presented a key for the separation of the species in this genus keeping *I. cubensis* and *I. arvicanthidis* as distinct species. Since then Mahon (1954) and Ezzat (1954) have described two further species in this genus, and also Mahon (1954) has shown that

the variation of the species in this genus is so great that the key of Joyeux and Baer (1949) in its present form is unreliable.

The nearest relative to *Inermicapsifer rhodesiensis* appears to be *I. arvicanthidis*. It is distinguished from Kofend's, Baylis', and Mahon's Belgian Congo material by its size, number of testes, size of cirrus-sac and the relative proportions of the various organs of the body. Mahon also described some material of this species at present in the collection of the Musée Royal du Congo Belge. This latter material, collected from rats and a mouse, has a very wide variation, but *I. rhodesiensis* may still be distinguished from it by the size of the cirrus-sac, the size of the testes, and the relative proportions of the various organs of the body, as seen in the table.

		<i>I. arvicanthidis</i>		<i>I. rhodesiensis</i>
		Baylis	Mahon (1)	Mahon (2)
Length	185 mm.	62-132
Breadth	3 mm.	2.5 mm.
Scolex45-.55	.37-.44
Suckers19	.14-.16
No. testes	48-55	20-78
Dia. testes06	.061-.072 ×
				.05-.065
Cirrus-sac...1-1.12 ×	.126-1.58 ×
			.06	.05-.061
Scolex/Segment ratio	...		1 : 2.8-6.7	1 : 5.8-11.4
Cirrus-sac/Segment ratio			1 : 10-17	1 : 22-46
Sucker/Scolex ratio	...		1 : 2.5-3.6	1 : 2.5-3.3
Ovary axis/Segment ratio			1 : 2-2.7	1 : 2-3

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A New Cestode, *Anomotaenia prinopsia* sp.nov. from the Straight Crested Helmet Shrike, *Prinops plumata*, in Southern Rhodesia

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Eleven cestode specimens were collected from the intestine of *Prinops plumata* which was brought into the Department for examination. They appear to be a new species for which the name *Anomotaenia prinopsia* is given.

DILEPIDIDAE Fuhrmann, 1907.

DILEPIDINAE Fuhrmann, 1907.

Anomotaenia Cohn, 1900.

Anomotaenia prinopsia sp.nov.

The worms are medium sized with a maximum length of 42 mm. and a maximum width of 0·87 mm.

The scolex has a diameter of 0·29-0·301 mm., and is provided with four very large circular unarmed suckers, measuring 0·137-0·142 mm. in diameter.

The rostellum is well defined, and when everted has a diameter of 0·06 mm. The rostellar sac is 0·129 mm. long \times 0·065 mm. wide. The rostellum is armed with twenty-one hooks, arranged in a double row, and measuring 39-40 μ in length.

The neck is very short. The margins of the segments are entire. The genital pores alternate irregularly opening in the anterior third of the segment.

The excretory system consists of a pair of narrow dorsal canals, and a pair of wider ventral canals, joined by a commissure in the posterior part of each segment.

There are two longitudinal nerve trunks situated laterally to the excretory canals.

The testes are 27–30 in number and are confined within the lateral excretory canals. They are 0·028–0·035 mm. in diameter. The vas deferens is very convoluted and leads directly into the cirrus pouch without forming an external seminal vesicle. The cirrus-sac is 0·154–0·172 mm. long \times 0·026–0·027 mm. wide. The average length is 0·16–0·162 mm. The cirrus-sac reaches the excretory canals, overlying the ventral canal. The cirrus is unarmed. The genital atrium is small, and non-muscular.

The vagina opens into the genital atrium behind the cirrus pouch, and follows a straight course to the receptaculum seminis. The genital ducts pass between the excretory vessels. The ovary is fairly large and lobed, the aporal lobe being slightly larger than the poral lobe. The vitelline gland is large, being 0·07 mm. wide \times 0·088 mm. in diameter. Mehlis' gland is small, but distinct, being 0·044 mm. in diameter. In the gravid segments the uterus becomes sac-like, and fills the segment. The eggs are thick-shelled, and measure 31–36 μ \times 42–49 μ . The embryonic hooks are 10–12 μ long.

Host : *Prinops plumata*.

Habitat : Intestine.

Locality : Nr. Salisbury, Southern Rhodesia.

Type to be deposited in the British Museum (Natural History).

DISCUSSION

The author has previously discussed the present systematic position of the genus *Anomotaenia* (see Mettrick, 1958).

There are at present seventeen species of *Anomotaenia* recorded from Passeriform birds. The new species described above can be easily differentiated from other species in the genus by reference to the number and size of the rostellar hooks, number of testes,

and the size of the cirrus-sac. Using these points, *Anomotaenia prinopsia* may be distinguished from the following species which appear to be related to it: *Anomotaenia borealis* (Krabbe, 1869), *A. constricta* (Molin, 1858), *A. murudensis* (Baylis, 1926), *A. trigonoccephala* (Krabbe, 1869), and *A. tarnograskii* (Dimmick, 1927).

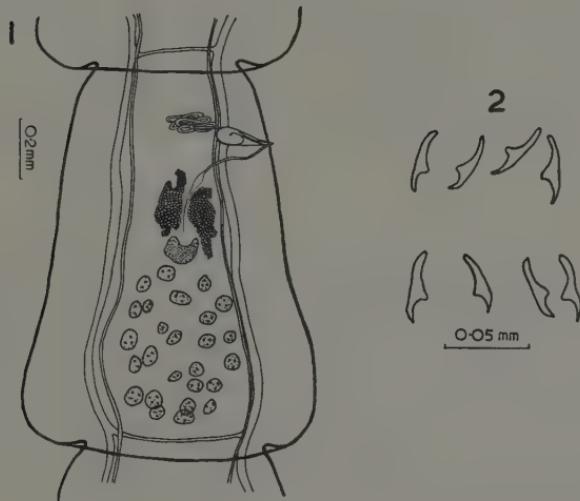


Fig. 1.—Mature segment of *Anomotaenia prinopsia*. Fig. 2—Rostellar hooks mounted in Berlese.

It is possible also that no fully gravid segments of *Anomotaenia prinopsia* were recovered and the uterus may, at a late stage, break down into egg capsules. In that case this new species should be placed in the genus *Choanotaenia* Railliet, 1896. Using the criteria listed above this new form may be differentiated from the species *Choanotaenia* recorded from Passeriform birds and in particular from *Choanotaenia galbulae* (Gmelin, 1790), *C. musculosa* (Fuhrmann, 1896), *C. spinasocapite* (Joyeux and Baer, 1955), and *C. microsoma* (Southwell, 1922).

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The Seasonal Availability to Sheep of Infective Nematode Larvae on Pasture

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Information was sought on the availability of nematode infective larvae to lambs during the summer and autumn under normal farm conditions.

Romney lambs reared worm free were exposed to risk of parasitism in the field to serve as indicators of the abundance of infective larvae.

Plan of the experiment

A flat ten acre paddock of permanent pasture, which had been grazed for some years by sheep, was chosen for the experiment. In the spring, before the experiment began, it was stocked by Southdown ewes and, from August onwards, also by their lambs. Prior to the test animals being placed in the paddock the extent of parasitism in the flock animals was determined by means of faecal egg counts.

Groups of four Romney lambs, reared worm free, were introduced in succession for two weeks of grazing from 7th December 1950, until 23rd May 1951. After removal from the paddock, each group of test lambs was killed immediately and replaced by another group of four. Data were collected in terms of the fourth and fifth instar worms found in the abomasum and small intestine. Sieves and dilution methods were used in picking out and counting worms.

The flock lambs were weaned early in January and their mothers removed. On 5th March the lambs also were taken from the paddock, and soon after were replaced by mature Southdown sheep. From this time on only the latter and test lambs occupied the paddock.

The flock ewes and their lambs received anthelmintic treatment in mid November.

As a supplementary investigation the degree of parasitism in Southdown ewes and their lambs in neighbouring paddocks was determined, by faecal examination.

Experimental lambs

The test lambs were reared indoors, their mothers being driven in a number of times daily to feed them. Transition in their diet was made completely to lucerne hay and a small amount of concentrates by 30th November.

A low degree of parasitism by *Strongyloides papillosus* and *Eimeria* spp. was unavoidable. Still smaller numbers of other parasites were acquired before the experiment began. At the beginning of the experiment the test lambs were approximately three months of age, with a variation of two weeks. The mean carcass weights (in pounds) of the groups of test lambs at the various killings were : Number 2 killing, 29.5 ; 3, 24 ; 5, 29.5 ; 6, 32.5 ; 7, 36 ; 8, 33.5 ; 9, 31.25 ; 10, 31.5.

Parasitism in the flock ewes and their lambs in the experimental paddock

On 7th November 6 ewes of the flock of 40 Southdowns were examined for parasitism, when up to 7,900 *Haemonchus contortus* eggs per gram faeces (e.p.g.) were found among individuals, the mean being 1,300. It is estimated that, in the spring until the beginning of the experiment, many hundred million eggs of this species had been conveyed to the ground in the experimental paddock. Other parasites found were *Ostertagia* spp., *Cooperia curticei* and *Strongyloides papillosus* but among none of these did counts exceed 100 e.p.g. A few eggs of *Nematodirus* spp. were found.

On 8th December, about three weeks after anthelmintics had been given, the mean egg count had dropped to 87 e.p.g. for the total of species, of which 9 were *H. contortus*.

Six of the flock lambs examined for parasitism on 11th November had a mean count of 1,295 e.p.g. consisting almost entirely of *Ostertagia* spp. and *Nematodirus* spp. *H. contortus* was present in small numbers. On 12th December, about three weeks after anthelmintics had been given, the mean count for 12 lambs was 479 e.p.g. Again *Ostertagia* spp. and *Nematodirus* spp. predominated with *H. contortus* occurring in low numbers.

Populations of worms found in the experimental lambs

The means, maxima and minima of the populations of nematodes found in the groups of lambs killed on the various dates during the experiment, between 7th December, 1950, and 23rd May 1951 are given in Table 1. As specific differences within genera in regard

to seasonal incidence were not apparent, the data have been assembled under generic headings. *Haemonchus contortus* outnumbered *H. placei*; *Ostertagia circumcincta* was more numerous than *O. trifurcata*; *Nematodirus filicollis* and *N. spathiger* occurred in similar numbers while *N. abnormalis* and *N. helveticus* were seldom found; *Trichostrongylus vitrinus*, *T. colubriformis* and *T. axei* were of similar order of abundance, and individuals of *Cooperia oncophora*, *C. mcmasteri*, *C. punctata* and *Bunostomum trigonocephalum* were found only sporadically.

Parasitism in sheep in neighbouring paddocks

Sixty-eight lactating Southdown ewes selected at random from a neighbouring flock were examined on 7th November. Among 22 of these, the total egg count ranged from 2,000 to 11,000 e.p.g. The mean count for the 68 ewes was 1,719 e.p.g. From a composite sample from the 68 ewes, the specific proportions of eggs using the scatter chart method (Tetley 1948) revealed that 82% were *H. contortus*, 16% *Ostertagia* spp. (possibly including a minority of *Trichostrongylus* spp.). The remaining 2% included *Cooperia curticei* and *Strongyloides* and perhaps *Chabertia ovina* and *Oesophagostomum venulosum*. *Nematodirus filicollis* and *N. spathiger* were found in two sheep, a total for the genus of 60 e.p.g. occurring in each.

One ewe, examined post mortem, contained 6,500 *H. contortus* adult worms and 7,500 *Ostertagia* spp. Another ewe in an exhausted state had an *H. contortus* egg count of 490,000 e.p.g., this animal is excluded from the above data.

The twenty eight lambs examined for parasitism had a mean count of all species of 732 e.p.g. Individual counts ranged from 0 to 3,000 e.p.g. The specific analysis obtained from a composite sample from these lambs was: *H. contortus*, 59 e.p.g.; *Nematodirus* spp. 254 e.p.g.; *Ostertagia* spp. 238 e.p.g.; *Strongyloides papilliferus* 180 e.p.g. Other species were singularly absent or in trace numbers.

DISCUSSION

Killing of the experimental lambs immediately after their removal from the paddock, while making the picking out of worms more difficult, provided a check on the efficacy of the method for rearing them worm free. With the exception of *Strongyloides papilliferus* there was no evidence, indicated by the presence of only mature worms, that pre-experimental infestation had taken place to a complicating extent.

Since lambs of the last group to be placed in the paddock were approximately six months older than these of the first group, there was the possibility that differences in the amount of grass eaten during the course of the experiment might have affected the results. If the intake of grass be proportional to the carcass weight, the mean group carcass weights, given above, indicate that there could not have been appreciable differences between the groups in exposure to risk of parasitism, other things being equal. Seasonal differences in the rate of grass growth, and the associated differences in the amount of foraging on the part of the lambs' thus possibly affecting degree of exposure, is a further problem. Reference to Table I shows that the population trends among the various species did not all run in unison nor did they parallel any expected seasonal differences in the amount of foraging of the lambs. It is concluded therefore that difference in age of lambs occasioned by the sequence in the experiment were not an invalidating factor.

In Table 1 it can be seen that *Ostertagia* spp. and *Nematodirus* spp. were acquired in greater numbers than other species. These two genera and *Haemonchus contortus* had well defined seasonal fluctuations in abundance.

Trichostrongylus spp. and *Cooperia* spp. occurred in smaller numbers than is customary among flock sheep and did not exhibit marked seasonal differences in incidence.

Nematodirus spp.

In the data presented on *Nematodirus* parasitism among Southdown ewes in the experimental and the neighbouring paddocks, it is shown that they acted in a minor capacity as hosts of this genus. This is consistent with results from other investigations (Tetley 1935, 1941, 1948) in which it was found that mature sheep seldom were infected and then with only small numbers.

The most obvious feature seen in the *Nematodirus* populations (Table 1) is that there was a steep rise to a peak after 1st March after which there was a return to numbers comparable with those in the early part of the experiment. It is notable that the peak occurred three to four weeks after the flock lambs, the source of eggs, were removed from the paddock.

To what extent infective larvae available between 1st December to 1st March, had survived from the previous autumn or were the result of the current season's eggs is not certain. Without doubt the rise in populations after 1st March was due to eggs from the flock lambs of the present season. Tetley (1935, 1941, 1948) found

TABLE 1

Populations of nematodes of the abomasum and the small intestine
of lambs after two weeks' exposure in the field.

Period	Killing date	Ost. spp.	Haem. spp.	Nemat. spp.	Trich. spp.	C. curt.	S. pap.
1	Dec. 21	(a)	130	15	64	0	5
		(b)	200	60	80	0	20
		(c)	80	0	20	0	0
2	Jan. 4	(a)	862	82	1,275	10	10
		(b)	1,130	160	1,710	10	10
		(c)	540	40	840	10	0
3	Jan. 18	(a)	1,310	180	177	33	66
		(b)	2,480	260	510	80	100
		(c)	440	60	0	0	0
4	Feb. 1	(a)	275	75	1,747	17	10
		(b)	380	200	2,640	50	30
		(c)	220	20	1,060	0	0
5	Feb. 15	(a)	175	10	673	11	7
		(b)	220	40	780	32	20
		(c)	140	0	500	0	0
6	Mar. 1	(a)	525	15	1,287	15	68
		(b)	780	40	2,140	20	110
		(c)	300	0	210	10	20
7	Mar. 14	(a)	430	20	3,270	7	7
		(b)	680	60	4,670	20	20
		(c)	140	0	1,970	0	0
8	Mar. 28	(a)	500	0	4,082	30	5
		(b)	580	0	5,700	50	10
		(c)	440	0	2,840	10	0
9	Apr. 11	(a)	332	0	3,247	55	37
		(b)	380	0	5,790	70	110
		(c)	260	0	1,110	40	10
10	Apr. 26	(a)	440	5	1,874	34	22
		(b)	720	20	4,110	55	44
		(c)	220	0	491	13	12
11	May 9	(a)	505	20	2,080	16	16
		(b)	740	60	4,660	30	30
		(c)	240	0	310	0	0
12	May 23	(a)	540	5	1,224	60	62
		(b)	860	20	1,580	180	120
		(c)	260	0	790	0	20

(a), (b) and (c) respectively means, maxima and minima of groups.

that ordinary spring born flock lambs usually develop resistance to super-infection by late summer or early autumn. The results in Table 1 show that large numbers of infective larvae were not available to the sheep until after early autumn. In another investigation Tetley (1959a) it was concluded that lambs, up until the end of January, did not bring about self augmentation of their *Nematodirus* parasitism.

From the foregoing it would appear that few if any eggs conveyed to pasture by lambs gave rise to infective larvae available to current members of the flock.

The predominance of *Nematodirus* spp. among the parasites acquired by the lambs towards the end of the experiment indicates that free-living stages of this genus were entering the winter in abundance. Elsewhere it has been shown (Tetley, 1959) that *Nematodirus* spp. may be acquired in large numbers by sheep in August as the result of over-wintering larvae.

Haemonchus contortus

It is shown in Table 1 that *H. contortus* was acquired in variable numbers throughout the experiment. The greatest were found for the periods ending on 4th January, 18th January and 1st February, the means being respectively 82, 180 and 75. During this six weeks 73% of the total of worms found during the experiment were picked up.

The intensity of *H. contortus* parasitism was low compared with that present in the ewes in the spring. It is estimated that some hundred million eggs of this species were conveyed to the ground in the spring before the beginning of the experiment by the ewes inhabiting this paddock. This high degree of contamination of the grass is clearly seen to have had no direct bearing on the extent of parasitism in the experimental lambs. Similarly among the neighbouring flock sheep the considerable pasture contamination with eggs in the spring by the ewes resulted in only small populations in their lambs, by 7th November. It is concluded that climatic conditions in the spring and early summer were not favourable for the development of infective larvae.

Dinaburg (1944) concluded that temperature was more significant than other factors of climate, notably humidity, in the development of *H. contortus* infective larvae. He found that when the monthly mean maxima exceeded 65°F. conditions were favourable for growth to the infective stage. In the present experiment the weekly mean maxima exceeded 65°F. from the beginning of November until the end of the following March, with the exception of the third week in November. Since populations of infective larvae were unable to build up under these conditions prescribed by Dinaburg it is possible that in New Zealand, the effect of the whole range of daily fluctuations in temperature must be considered in order to assess the degree of the favourability of the environment for the free living stages of this species.

Ostertagia spp.

Thirty-six per cent of *Ostertagia* spp. found in the lambs were acquired between 21st December and 18th January. Thereafter these species occurred in relatively low, uniform numbers. Thus the 21st December to 18th January period was a particularly favourable one for the development of infective larvae. However, the uniformity with which the parasites were acquired after this period indicates that many infective larvae were able to develop throughout the experiment.

There is uncertainty as to when resistance to superinfection is invoked against this genus but the data accord with other investigations (Tetley, 1959a) in which it was concluded that self augmentation of parasitism is able to occur in lambs in summer.

In common with *Nematodirus* spp. it is seen in Table 1 that *Ostertagia* spp. were relatively abundantly acquired until the end of the experiment and therefore the stage was set for many infective larvae to over-winter on the ground.

SUMMARY

The seasonal availability of sheep nematode infective larvae under normal farm conditions was investigated by exposing lambs reared worm free for two weekly periods in the fields. Data were collected in the form of populations found at post mortem examination.

It was found that *Nematodirus* spp. were acquired in greatest numbers in the autumn after the date by which lambs normally have acquired resistance to superinfection. The conclusion was that self-augmentation of *Nematodirus* parasitism in lambs resulting from eggs the lambs conveyed to the ground was of minor significance and that eggs reaching the ground in one season are the source of parasitism in lambs in the following spring.

It was found that greatest numbers of *Haemonchus contortus* were acquired in summer. Heavy contamination of pasture with eggs of this species by ewes in the spring did not result in large populations in their lambs. It was concluded that the extent of parasitism in lambs in the late summer and autumn was contingent on there being favourable conditions at that time of the year for the development of infective larvae.

Ostertagia spp. were acquired in greatest numbers in summer and results were consistent with self-augmentation of parasitism in flock lambs having been possible.

Trichostrongylus spp. and *Cooperia curticei* occurred in small numbers and did not display seasonal differences in incidence during the six months duration of the experiment.

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The Availability of the Infective Stages of Nematode Parasites to Sheep in Early Spring

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In New Zealand, *Ostertagia circumcincta*, *O. trifurcata*, *Nematodirus filicollis* and *N. spathiger* considerably outnumber other parasitic nematodes in spring born lambs in early life (Tetley, 1934, 1941, 1948). The belief that this incidence is purely a function of the availability of infective larvae has been incompletely tested.

In order to obtain some knowledge of the relative number of infective larvae of the various species available to lambs in early spring the following experiment, using previously uninfected grown sheep as indicators, was carried out.

Experiment 1: On 10th August 1949, eight eleven month old Romney sheep which had been reared free of parasitism were placed in a Massey College sheep farm paddock which had been grazed for a number of years according to normal farm practice. Twenty-one days later the sheep were killed and the fifth instar worms of the abomasum and the small intestine counted. Results are given in Table 1.

The species found were *Ostertagia circumcincta*, *O. trifurcata*, *Nematodirus filicollis*, *N. spathiger*, *Trichostrongylus colubriformis*, *T. vitrinus*, *Cooperia curticei* and *Strongyloides papillosus*.

During the following summer and autumn populations of *Haemonchus contortus*, *Trichostrongylus* spp. and *Cooperia curticei* as well as *Nematodirus* and *Ostertagia* species rose to high levels among flock sheep of the College farm, in some instances totals of over 50,000 worms being found.

DISCUSSION

Experiments of this type require to be repeated many times before conclusions may be drawn with finality.

Tetley (1948, 1957), found that all species of nematodes parasitic in sheep in New Zealand were able to establish themselves in previously uninfected sheep of similar age to the present test animals. The present results, therefore, may be taken as a reliable guide to the availability of infective larvae.

From Table 1 it can be seen that *Ostertagia* and *Nematodirus* species predominated; other species occurred in small numbers. This order of parasitism closely resembles that found normally in spring born flock lambs in early life (Tetley 1934, 1941, 1948) and indicates that the incidence in the latter is determined primarily by the availability of infective larvae.

TABLE 1

Populations of nematodes found in the stomach and small intestine of 11 months old sheep after being exposed in the field for 3 weeks from 10th August 1949.

Sheep No.	<i>Ost.</i> spp.	<i>H. cont.</i>	<i>Nem.</i> spp.	<i>Trich.</i> spp.	<i>C. curt.</i>	<i>S. pap.</i>
1	410	10	590	40	30	10
2	795	0	1,540	70	20	50
3	650	5	?	10	?	?
4	685	0	65	20	0	0
5	755	0	850	10	30	0
6	1,430	5	1,400	60	0	0
7	370	0	510	20	30	10
8	345	0	220	10	20	10

The results of this experiment accord with previous findings of the writer (*ibid*), and of a number of others, whose work has been reviewed by Kates (1950), that *Ostertagia* and *Nematodirus* are able to over-winter on the ground in greater numbers than other genera. It is reasonable to conclude that the high incidence of these genera in spring lambs is due to the large number of over-wintering infective larvae on pasture. This being true, the early spring numbers of infective larvae on grass provide a means for forecasting the intensity of their parasitism in the lambs in the first few months of life.

It has been previously mentioned that parasitism by *H. contortus*, *Trichostrongylus* spp. and *C. curticei* rose to a high level on the College farm including the experimental area, in the following summer and autumn. This fact is suggestive that the intensity of parasitism by these species in lambs in summer and autumn was not directly correlated with the numbers of infective larvae available in the spring. Among these genera it would appear that small numbers of over-wintering larvae may perpetuate the species and that initial low intensity of parasitism in lambs associated with a process of self-augmentation of parasitism may result in heavy infestation later in the summer. Should this be correct then forecasting of abundance of these species in lambs must depend on study of the self-augmentation process of parasitism in relation to climate rather than by study of spring incidence of infective larvae on pasture.

SUMMARY

Previously uninfected eleven month old sheep were used as indicators of the availability of the infective larvae of sheep nematodes in early spring. *Ostertagia* and *Nematodirus* species were acquired in much larger numbers than other species. It is concluded, since the order of parasitism found in the experimental sheep resembled that found in spring born flock lambs in early life, that the relative specific incidence is the latter is due to the numbers of available infective larvae and not to any factor associated with the stage of development of the lambs.

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The Extent to which Self-Augmentation of Nematode Parasitism Occurs in Lambs

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Self-augmentation is defined as the growth of parasite populations in hosts resulting from eggs emanating from existing parasites in members of the same flock.

It is common husbandry practice to move farm stock to fresh pasture as frequently as possible with the intention of avoiding high intensity of nematode parasitism. Such a programme of animal management has as a basis, knowledge of the life histories of the parasites. Many workers have investigated the factors which influence the development of parasites during their free-living existence. Of these, Dinaburg (1944) and Kates (1950) may be singled out, partly because their work is distinguished and partly for their reviews of the work of others. This work makes it apparent that more than a literal interpretation of the bare facts of the life cycles is required if the incidence of parasitism in farm animals is to be understood and schemes for avoiding heavy parasitism are to be effectively applied.

The present experiments were carried out in order to obtain knowledge of the extent to which self-augmentation of nematode parasitism takes place in lambs.

The earliest work in this field, so far as the writer is aware, is that of Stoll (1932), who studied *Haemonchus contortus* population growth in sheep.

Plan of the Experiment

Data were sought on the availability of nematode infective larvae from soon after the time that eggs first appear in the faeces of spring born lambs and through the period of rapid accumulation of parasites in these animals. To this end, lambs and grown sheep

reared from birth, worm free, were used as indicators on a selected paddock grazed according to ordinary farm practice by flock ewes and their lambs. Data were collected in terms of populations of fourth and fifth instar worms found in the test animals at post mortem examination after three weeks' exposure in the paddock. The three periods of the experiment were initiated on 29th November, 20th December and 10th January.

Twelve weaned lambs were placed in the field on each of the given data together with, respectively, 4, 6 and 5 grown sheep.

Experimental Sheep

Romney sheep were used. The lambs were spring born and three to four months old at the initiation of the experiment. The grown sheep ranged in age from 1 year 3 months to 3 years 3 months. Six of the latter were given small populations of *Haemonchus contortus* approximately one year before, which had been eliminated, either naturally or by anthelmintics, several months prior to the beginning of the experiment.

Results

The following species were found in the abomasum and small intestine of the test sheep :—

Haemonchus contortus, *Ostertagia circumincta*, *O. trifurcata*, *Strongyloides papillosus*, *Trichostrongylus axei*, *T. vitrinus*, *T. colu biformis*, *Nematodirus filicollis*, *N. spathiger*, *Cooperia curticei*, *C. oncophora*, and *C. mcmasteri*.

These have been established under generic headings in the data as no specific differences of significance in the present connection were apparent.

The populations of *Nematodirus* and *Ostertagia* found in the spring born lambs are contained in Table I. The means for three of the genera occurring in small numbers in these animals, for the three periods of the experiment, follow in chronological order : *Haemonchus*, 74, 28, 64; *Trichostrongylus* spp., 65, 6, 54; *Cooperia* spp., 69, 44, 248. *Strongyloides* occurred in still smaller numbers.

The results from the grown sheep are given in Table 2.

Discussions and Conclusions

Tetley (1935, 1948) found that resistance to superinfection by *Nematodirus* spp. in spring born lambs became effective in late summer and early autumn. The evidence for *Ostertagia* spp., less clear cut, suggested that resistance to superinfection developed about the same time. The present experiments, therefore, may be regarded as covering a period before such resistance normally comes into operation in spring born flock sheep.

TABLE I

Populations of *Ostertagia* spp. and *Nematodirus* spp. found in weaner lambs after three weeks' exposure in the field.

Nov. 29—Dec. 20			Dec. 20—Jan. 10			Jan 10—Jan. 31		
Sheep No.	<i>Ost.</i> spp.	<i>Nemat.</i> spp.	Sheep No.	<i>Ost.</i> spp.	<i>Nemat.</i> spp.	Sheep No.	<i>Ost.</i> spp.	<i>Nemat.</i> spp.
9	1,300	2,220	1	480	?	3	660	552
10	2,480	2,960	6	1,040	660	5	3,400	?
14	160	40	7	460	320	12	2,120	1,520
17	2,420	2,080	8	300	40	18	3,370	?
22	1,020	620	13	1,440	800	21	4,680	1,304
24	1,740	280	19	640	380	31	2,140	144
27	880	1,020	20	1,460	40	32	1,410	110
33	840	660	26	1,120	480	34	3,000	1,100
38	1,520	?	37	1,660	320	36	1,660	1,930
40	300	140	41	2,700	980	39	420	?
45	580	1,160	49	2,580	1,500	44	1,730	784
51	1,580	2,180	50	1,420	760	46	1,440	990
Mean	1,235	1,215		1,275	572		2,169	939
Maximum	2,480	2,960		2,700	1,500		4,680	1,930
Minimum	160	40		460	40		420	110

Nematodirus spp.

The present experiment took place in early and mid summer after spring born flock lambs had become infected with *Nematodirus*.

This raises the question of the proportion of worms, found in the test animals, that had origin in over wintering larvae or had been derived from eggs conveyed to the ground in the current season.

Tetley (1948) found that the numbers of eggs of all nematode species occurred in relatively small numbers in the faeces of spring

born flock lambs until at least the end of November. Kates (1950) established that several weeks may be required after deposition of *Nematodirus* eggs before infective larvae become available to sheep. It is concluded, therefore, in the present experiment, that insufficient time had elapsed before its initiation on 29th November, for many infective larvae to have developed from eggs of the current season and to have become available to sheep.

Nematodirus infective larvae are long lived, as Tetley (1948) and Kates (1950) have shown. In New Zealand they may survive in large numbers through the winter until, at least, the following autumn. The former author (1959) found that in early spring populations of over-wintering *Nematodirus* infective larvae on pasture, as shown by numbers of worms acquired by test animals, considerably outnumbered other species, with the exception of *Ostertagia* spp. It is therefore reasonable to draw the conclusion that the populations of this genus acquired by experimental sheep in the first period of experiment, at least, were mainly if not entirely, of over-wintering origin.

Mean population of *Nematodirus* in grown sheep (Table 2) show a sharp fall between the first and second periods of the experiment and a smaller one between the second and third. That is, the intensity of the population of infective larvae to which the lambs were exposed diminished during the experiment. The data for the lambs (Table I) do not show such an abrupt fall in the succeeding periods. There can be no doubt that the lambs were exposed to the same intensity of infective larval populations as the grown sheep. The difference between the two groups in numbers of worms found at post mortem examination is explained by the fact that the lambs grew rapidly during the experiment and the grown sheep at a slower rate. Associated with rapid growth, the lambs ate grass in increasing quantities and their exposure to risk of parasitism must also have increased. In the light of this consideration the tendency for a decline in the number of worms acquired by the lambs is translated into a definite fall. With the onset of summer the rate of growth of grass diminished and both groups of animals required to take more bites of food thus further increasing their exposure to risk of parasitism, other things being equal.

The downward trend in the *Nematodirus* populations in the experimental sheep runs counter to the upward trend that occurs in numbers of eggs of this genus in the faeces of flock lambs at this time of the year (Tetley 1935, 1948). The conclusion follows that

TABLE II
Populations of nematodes found in the abomasum and small intestine of grown sheep after three weeks' exposure in the field.

Period	Sheep No.	Age	Ostertagia spp.	Nematodirus spp.	Haemonchus contortus	Cooperia curvicauda	Trichostrongylus spp.
Nov. 29—Dec. 20	44/30 *136	1yr. 3mths. 1yr. 3mths.	3,320 2,580	5,520 6,980	60 60	240 114	80 145
	44/5	2yrs. 3mths.	160	3,340	20	100	100
	44/2	2yrs. 3mths.	2,100	2,800	80	80	180
	Mean		2,040	4,660	55	134	141
Dec. 20—Jan. 10	43/43 44/36 *44/35	1yr. 4mths. 1yr. 4mths. 1yr. 4mths.	1,060 1,380 440	?	?	?	?
	44/15 56	2yrs. 4mths. 2yrs. 4mths.	4,460 3,540	820 2,260	20 20 plus	80 140	60 0
	29/3	3yrs. 4mths.	1,400	220	60	220	100
	Mean		2,037	680	0	20	240
				868	20	115	80
Jan. 10—Jan. 31	*44/40 *44/24 *848 *44/31 16	1yr. 5mths. 1yr. 5mths. 1yr. 5mths. 1yr. 5mths. 2yrs. 4mths.	1,830 5,330 1,090 2,120 70	1,265 720 600 432 330	0 120 50 30 0	910 480 500 192 110	130 0 60 104 10
	Mean			2,088	669	40	438
							61

* Sheep infected in 1955 with small numbers of *H. contortus* which had been eliminated subsequently, either naturally or by anthelmintics.

self-augmentation of *Nematodirus* infestation could either not have been taking place in the ordinary flock during the present experiment, or could have been occurring only to a small degree. Support for this is given by Thomas (1956) whose data indicate that eggs of this genus conveyed to pasture in Britain do not give rise to infective larvae available to lambs until the following spring.

Ostertagia spp.

Ostertagia mean populations in grown sheep (Table 2) remained almost constant during the three periods of the experiment, thus showing that the intensity of infective larval numbers was maintained at a near constant pitch. Among the lambs (Table 1) the upward trend at the final killing is accountable for in terms of the increasing exposure to risk of parasitism through progressively greater intake of grass.

As with *Nematodirus* it is probable that at the initiation of the experiment many of the infective larvae acquired were of overwintering origin. It is inconceivable however that the intensity of the overwintering larval population could maintain at a constant pitch until the final killing of the experimental animals. The heavy grazing of approximately four ewes and their lambs for several weeks as well as the mortality among infective larvae would take a heavy toll of the population. It is concluded, therefore, that eggs conveyed to the ground in the current season were developing to the infective stage and becoming available to sheep. That is, a process of self-augmentation of *Ostertagia* parasitism was taking place in the flock lambs. Since grown sheep may harbour this genus there is doubt on the relative roles of the ewes and the lambs in giving rise to the population of infective larvae.

Species found in small numbers

Since *Haemonchus contortus*, *Trichostrongylus* spp., *Strongyloides papillosus*, and *Cooperia* spp. occurred in very small numbers and did not display any marked trend it is concluded that any self augmentation process of parasitism among flock lambs must have been of insignificance. This conclusion is consistent with other findings (Tetley, 1948) that these species do not begin to accumulate in large numbers in spring born lambs until after mid summer, with the possible exception of *H. contortus*.

The upward trend in *C. curticei* populations in the grown sheep was a departure from what occurred in the lambs. Frequently this species may not achieve peak numbers until the second year of life of sheep (Tetley 1934, 1941, 1948) and it is possible that some inhibitory factor operates against it in young animals.

SUMMARY

Sheep reared worm free were used as indicators of the availability of sheep nematode infective larvae during the summer on pasture grazed by ordinary flock ewes and their lambs.

Data were collected in terms of worms found in the test sheep at post mortem examination after periods of three weeks' exposure in the field.

Ostertagia and *Nematodirus* species considerably outnumbered *Haemonchus contortus*, *Trichostrongylus* spp., *Cooperia* spp. and *Strongyloides papillosus*.

It is concluded that, for this particular period and year, self-augmentation of *Ostertagia* parasitism took place in lambs.

The process did not occur, or only to minor extent, with other species prior to mid summer.

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Development of *Haemonchus contortus* in Weaned and Unweaned Lambs

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Porter (1941) found that milk in the diet of young cattle inhibited the development of *Haemonchus contortus*, a result he attributed to the direct effect of milk on the parasites in the abomasum. Whitton (1954) suggested that the lower incidence of pig parasitism in the North Island compared with the South Island of New Zealand might be due to the greater extent that pigs were fed milk and milk products in the former.

In New Zealand, where spring lambing is the practice, *H. contortus* is absent from, or occurs in low numbers in unweaned lambs still receiving much milk from their mothers. This might be held to be due to the unavailability of infective larvae in the cool New Zealand spring, were it not that in some springs, lactating ewes, particularly Southdowns, may have large populations of this parasite, presumably acquired in late winter or early spring.

In countries such as Australia, where autumn lambing takes place, this parasite may be abundant in merino lambs before weaning. This fact would suggest that milk does not inhibit parasitism. However, Romneys, the predominant breed in New Zealand, produce much more milk than Merinos and the possibility exists that the quantity or some quality of milk that lambs of the former receive, might exert an influence on the incidence of *H. contortus*.

The following experiments with Romney sheep were therefore carried out to determine to what extent milk played a part in modifying the incidence of *H. contortus* in the early stage of parasitism.

METHODS

Known numbers of *H. contortus* infective larvae were given to (a) unweaned lambs and to (b) weaned lambs, all of which were reared worm free. Data were collected in terms of fourth and fifth instar worms found at post mortem examination, nine to twenty-one days after infections were given. Unless otherwise stated unweaned lambs received a supplementary diet of lucerne hay and concentrates. Weaned lambs received lucerne hay and concentrates. When infective larvae were given in water, the volume was of the order of 10–25 mls. In some experiments larvae were administered on damp filter paper.

EXPERIMENTS

A. Unweaned Lambs

Experiment 1: Four six weeks' old lambs were each given 2,200 freshly emerged *H. contortus* infective larvae in water on 14th October 1952. The milk production by their mothers was at a high level. Fourteen days later the lambs were killed. The populations of *H. contortus* found are given in Table 1.

Experiment 2: Five six-weeks' old lambs, reared with those of experiment 1, were each given 1,000 freshly emerged *H. contortus* infective larvae in water on 31st October 1952, by which date the milk production of their mothers, though abundant, had declined. The lambs were killed fourteen days later. The results are given in Table 1.

Experiment 3: Eight ten weeks' old lambs were given 1,000 freshly emerged *H. contortus* infective larvae in water on 9th November 1945, when milk production by their mothers had fallen considerably. The lambs were killed twenty-one days later. The results are given in Table 1.

B. Weaned Lambs

Experiment 4: Following weaning, 42 six month old lambs were reared on lucerne hay and a small amount of concentrates. On 21st February 1952, they were placed on plots of grass and clover free from infective larvae. Four days later, each lamb was

TABLE I

Lamb No.	Number of <i>H. contortus</i> given	Number <i>H. contortus</i> at post mortem	Per cent. recovery rate	Group mean (per cent)
UNWEANED LAMBS				
<i>Experiment 1 :</i>				
1	2,200	879	40	
2	2,200	50	2	
3	2,200	2,125	96	
4	2,200	1,213	55	48
<i>Experiment 2 :</i>				
5	1,000	756	76	
6	1,000	691	69	
7	1,000	343	34	
8	1,000	395	40	
9	1,000	699	70	58
<i>Experiment 3 :</i>				
22	1,000	43	4	
23	1,000	376	38	
27	1,000	200	20	
29	1,000	81	8	
33	1,000	306	31	
34	1,000	5	1	
38	1,000	376	38	
139	1,000	100	10	19
WEANED LAMBS				
<i>Experiment 4 :</i>				
42	2,000 range	19-905 Range	10-45	30
<i>Experiment 5 :</i>				
77	1,000 Range	190-1130 Range	19-100	64

* The high number is attributable to dilution methods having been used in measuring doses of infective larvae.

given 2,000 freshly emerged *H. contortus* infective larvae on filter paper. After a further fourteen days, the lambs were killed. The numbers of worms found at post mortem ranged from 10 to 45% of the larvae given, 30% being the average.

Experiment 5 : Seventy-seven three month old lambs, immediately following weaning, on 25th November 1953 were placed on plots of grass and clover free from infective larvae. Six days later they were each given 1,000 *H. contortus* freshly emerged infective larvae on filter paper. The populations found at post mortem, on 10th December, nine days later, ranged from 19 to 100% of the larvae given, the average being 64%.

DISCUSSION

Veglia (1915) is ambiguous on the question of whether *H. contortus* infective larvae are able to exsheath in the abomasum of sheep. Sommerville (1954), investigating *H. contortus* and other species, obtained results suggesting—"that the infective larvae of species normally parasitic in sheep commence to exsheath in that part of the intestinal (sic) tract which immediately precedes the region in which the adults are normally found." He goes on to say that *H. contortus* was observed to exsheath in the rumen. He has informed me since that larvae will not exsheath in the abomasum.

Since fluids may or may not enter the rumen there is the possibility that some larvae given in experiments 1-3 by-passed the rumen and entered the abomasum without exsheathing, and thus were not able to establish themselves. In experiments 4 and 5, larvae were given on damp filter paper and there is a greater degree of certainty that they entered the rumen and exsheathed in the normal way.

Among lambs receiving milk the numbers of worms found, among the various experiments, ranged from 1-96% of infective larvae given, and for weaned lambs, from 10-100%. The mean percentages for the three experiments on unweaned lambs were 48, 58 and 19, while for weaned lambs they were 30 and 64. Since different cultures of *H. contortus* may vary in survival potential it is concluded that the above results do not indicate differences between unweaned and weaned lambs in favourability as hosts.

SUMMARY

Haemonchus contortus infective larvae were given to previously uninfected weaned and unweaned romney lambs. Difference in susceptibility between the groups was not found.

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DATES OF PUBLICATION FOR VOLUME XXXII

Nos. 1/2	30th June 1958
No. 3	20th October 1958
No. 4	31st December 1958

CORRIGENDA IN VOLUME XXXII

Page 221—Legend to figure should read "Fig. 5".

Page 223—Legend to figure should read "Fig. 3".

Page 272—for "*MORGASCARIDA*" read "*MORGASCARIDIA*".

